IX. *On the Phylogeny of the* Pierinæ, *as illustrated by their Wing-markings and Geographical Distribution.*

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I. Introductory.

In the present paper my object has been to apply to the study of the subfamily *Pierinæ* the methods which I used in investigating the phylogenetic relations of another group of Lepidoptera, as recorded in a former communication to this Society.* I have in the first place endeavoured to work out the homology of the various

* "On the Phylogenetic Significance of the Wing-markings in certain genera of the Nymphalidæ," Trans. Ent. Soc. Lond., 1890.

markings to be found throughout the group, and have then attempted to state the phylogenetic conclusions to which this evidence appears to lead. Though my principal aim has been the elucidation of the Pierine wing-markings, which so far as I am aware have never before been systematically studied from this point of view, I have not ignored those other features that are usually known as "structural"; and I have also tried to estimate the bearing upon phylogenetic questions of the facts relating to the present distribution of the *Pierinæ* in space. The serious limitations under which anyone who wishes to construct a phylogeny for such a group as this must necessarily labour have been elsewhere acknowledged; it is of course manifest that little or no help can be expected from embryological or palæontological sources. There are, however, many compensating features to be reckoned on the other side; and in view of certain comments that have at times been passed on previous work of this kind, I may perhaps be allowed to quote a few sentences from the writings of one of our leading naturalists, which seem to me to state the special advantages afforded by these and similar researches with a force and cogency that it would not be easy to gainsay. After pointing out the pre-eminent value of the Diurnal Lepidoptera to the student of distribution and variation, the writer I refer to proceeds as follows—"But besides their abundance, their universal distribution, and the great attention that has been paid to them, these insects have other qualities that especially adapt them to elucidate the branches of inquiry already alluded to. These are the immense development and peculiar structure of the wings, which not only vary in form more than those of any other insects, but offer on both surfaces an endless variety of pattern, colouring, and texture. . . . This delicately painted surface acts as a register of the minutest differences of organization,—a shade of colour, an additional streak or spot, a slight modification of outline continually recurring with the greatest regularity and fixity, while the body and all its other members exhibit no appreciable change. The wings of butterflies, as Mr. Bates has well put it,* 'serve as a tablet on which Nature writes the

* See "The Naturalist on the Amazons," 2nd edit., p. 412.

story of the modifications of species'; they enable us to perceive changes that would otherwise be uncertain and difficult of observation, and exhibit to us on an enlarged scale the effects of the climatal and other physical conditions which influence more or less profoundly the organization of every living thing."* Whether any particular investigator is or is not competent to undertake this kind of research may be open to question, but I think that the study itself needs no further vindication than these words of Mr. Wallace.

In treating of the details of the wing-markings I have tried to be intelligible and explicit, even at the cost of being somewhat lengthy. I have, however, been obliged to content myself with selected examples; a complete treatment would run to a vast length, and in most cases the lines here laid down may be easily applied to the insects not mentioned in this paper. Some of the identifications of markings may at first sight seem startling; for instance, that of the straight orange-coloured line crossing the disc of the wings in *Dercas* with the series of black spots in the females of *Ganoris*; but I believe that in every such case it will be found that the homology can be certainly traced, step by step. It is hardly necessary to point out the importance of being on one's guard against the misleading suggestions of merely superficial resemblances, and also of giving due weight to the disturbing influence of mimicry. The details of this latter process, when minutely examined in a favourable group such as the *Pierinæ*, are seen to be of so complicated and interesting a character, that I may hope to be excused for having treated of some of these details with considerable fulness, and even for having ventured to introduce a new term in order to distinguish a special case of the phenomenon known as "Convergence."†

The generic names employed in this paper are those of Mr. Butler in his well-known "Revision" (Cistula Entomologica, vol. i., 1870, p. 33), supplemented by subsequent memoirs from the hand of the same author, and

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* "On the Papilionidæ of the Malayan Region," Trans. Linn. Soc., xxv., p. 1 (1866).

† See page 298.

by the arrangement at present adopted in the National Collection under his charge. I confess that I am not always in agreement with this arrangement, but the importance of a definite and accessible standard is obvious, and no better one could be found for my purpose. Even if the genera are not in every instance distinguished by characters of real "generic value," they are usually natural groups, and in most cases of great convenience in practice. The list of genera and species which I have appended may be found useful as indicating the exact insects which are mentioned in the course of the paper, and also as giving an idea of the scope and contents of those genera whose names may still be somewhat unfamiliar. A paper of this kind is not the place in which to introduce changes of nomenclature or to discuss questions of synonymy; and as regards classification I have done no more than throw out a few suggestions which, perhaps, may one day be taken up.

II. The Wing-markings.

1. *The submarginal series of dark spots.*

Comparing together the three species of the subfamily *Pierinæ* that are commonest in this country, viz., *Ganoris brassicæ*, *G. rapæ*, and *G. napi*, we find that the females of all three resemble one another in the possession of a series of black spots on the upper surface of the forewing. One of these spots (Fig. 16, S 8) occurs between the second and third median nervules; another (ibid., S 10), between the first median nervule and the submedian nervure; and the third (ibid., S 11) between the submedian nervure and the inner margin of the wing. The latter spot, which varies considerably in the amount of its development, takes the form of a streak nearly parallel with the inner margin. In the males, this series of spots is evanescent. The whole series is normally absent in *G. brassicæ* ♂, and in some specimens of *G. rapæ* ♂, and *G. napi* ♂; the males of the two latter species, however, generally have the spot between the second and third median nervule more or less developed, though the other two are not present. Turning to the underside of the wing in these species, we find the first two spots usually present in both males and females;

the third is but faintly visible in the female, and in the male not visible at all. These three spots are all that can be seen in ordinary specimens of *G. brassicæ, rapæ,* and *napi;* but in some specimens of *G. napi,* and less distinctly in some of *G. rapæ,* the series is continued towards the anterior border of the wing by a fourth spot placed just behind the junction of the third and fourth subcostal nervules, and traversed by the first discoidal. The spots that have now been referred to can be seen in a very well-marked form in *G. gliciria.*

These indications of a submarginal series of black markings become more pronounced in *Synchloe daplidice.* Here, in the female, a submarginal row exists in easily recognisable form, three of the constituent spots of which are clearly homologous with those already described in *G. napi, rapæ,* and *brassicæ* (Fig. 15). In this region of the wing nearly every interspace between nervules contains a spot; the spots tending to become confluent, especially towards the costal margin. There is generally no spot between the first and second median nervules, and often none between the submedian nervure and the inner margin of the wing. In the male, the anterior portion of the series is distinct enough, the large spot, however, between the submedian nervure and first median nervule is absent from the upper surface, though regularly present beneath. The female *S. daplidice* also shows a continuation of the same series on the hindwing, well-marked at the costa, but usually becoming less plain as the anal angle is approached. In the male *S. daplidice,* one term of the series is generally all that is present in the hindwing; and turning back to *G. brassicæ, rapæ,* and *napi,* we find the same spot invariably present on the upper, and often on the lower surface of the costa in the hindwing of both sexes (Figs. 15, 16, S 14—18).

Other species of the genus *Synchloe* present the same submarginal series in greater completeness. *S. callidice* ♀, for instance, has the whole series well developed on the forewing, and in most specimens on the hindwing also. A comparison with *S. daplidice* will show that the series is really homologous in the two cases, and will, moreover, demonstrate that in *S. callidice* the smallest spot of the series belongs to the interspace between the first and second median nervules, which in *S. daplidice* is usually

not furnished with a spot at all; and that the largest and best-marked member of the group, namely that between the second and third median nervules, corresponds with the spot which we saw to be most persistent in the males of *G. brassicæ*, *rapæ*, and *napi*. This spot, moreover, as well as the next most persistent (that between the first median and submedian), is usually picked out with black on the underside of both *S. callidice* and *S. daplidice*, where the markings corresponding to those of the upper surface are, as a rule, chiefly composed of green or yellow scales with but small admixture of black. The hindwing of *S. callidice* ♀ shows a continuation of the series; though here the markings as they approach the inner margin tend to assume the appearance of chevrons rather than of spots, which tendency is still more marked on the underside.

The South American genus *Tatochila* presents the same series on both fore and hindwings, the females as a rule most completely (as in *T. autodice*). The male of *T. theodice*, however, exhibits the whole series quite plainly; and in both of these species the markings in question tend to assume the form of a line of chevrons, the apices of which point towards the margin of the wing, instead of towards the base, as in *S. callidice*.

I propose to distinguish this series of spots as S (for Submarginal), numbering the constituent markings according to the interspaces they respectively occupy. In all the forms as yet mentioned the full number of marginal interspaces, from the costal nervure to the anal angle, is in the forewing 11, in the hindwing 8. Another space may be reckoned in the hindwing, that, namely, between the costal margin and the costal nervure. The corresponding space in the forewing is exceedingly narrow, and never carries a separate spot. We may take then the number of spaces potentially containing spots as 11 and 9 in the fore and hindwing respectively, and may designate all possible terms of the series as S 1—20, beginning at the costa of the forewing. None of the species above referred to exhibits the whole range of spots from 1 to 20 in a discrete condition, some being generally absent and others fused; the series may, however, be seen complete on the upper surface of the forewing and lower surface of the hindwing in many specimens of *Callidryas philea* and *C. thalestris* ♀ (Fig. 22, S 1—11).

In certain genera (*Eronia, Euchloe,* etc.), the presence of a fifth subcostal nervule gives rise to an additional interspace in the forewing; this, however, causes no difficulty, inasmuch as the extra interspace so formed is never occupied by a distinct spot. If necessary, the additional subcostal interspace may be referred to as 5a; by which plan we shall avoid throwing the numbering out of correspondence with that adopted in the other genera (see Fig. 23). In those genera (*Pereute, Delias,* etc.) which possess only three subcostal nervules in the forewing, I shall for convenience consider S 4 as absent.

Having identified the series S in the species named, we shall find no difficulty with the remaining members of the genera *Synchloe* and *Tatochila,* all of which possess it in a condition of greater or less development. In all these cases, if the sexes differ, the female invariably presents the series in greater completeness; though such of the spots as are present in the male are sometimes more distinct. Thus in *S. hellica* ♀, the whole range occurs with the exception of S 9 (this being also the spot which is regularly small or absent in *S. callidice* and *S. daplidice* ♀), and the spots show a great tendency to fuse into a submarginal band, especially towards the costa of the forewing. In the male, however, all are absent from the hindwing, and S 9—11 also from the forewing; S 8 is distinct; S 7 hardly visible; and S 2—5 are fused into a single spot which is more distinct than the corresponding patch in the female.

The same submarginal series can be traced with equal certainty in the genus *Belenois.* Here again the series is as a rule more complete in the females, while the individual spots are more distinct in the males. This can be well seen for example in *B. mesentina* (Fig. 13), where the males show a submarginal band on the forewing which can without difficulty be resolved into a series of five spots, representing S 2—3, 5, 6, 7 and 8. On the upper surface of the females the spots show a greater tendency to fuse with one another, and with the dark area of the apex and hindmargin; they are nevertheless in most specimens recognizable on the upper surface, and nearly always fairly distinct beneath. Much the same is the case with the submarginal series on the hindwing; this is constantly present in a distinct form on the under surface of both

sexes, and also to a variable extent on the upper surface of the male. The whole range (except the last member, S 20) occurs constantly on the upper surface in the female, but shows a strong tendency to fuse with the dark marginal band of the wing. In both male and female of this species the conspicuous and persistent spot S 8 occupies a prominent position, being pushed back as it were towards the centre of the wing, and so causing an indentation in the submarginal row. In *B. severina* the series is generally less well-marked than in *B. mesentina*, being to a great extent fused with the dark marginal band; S 10 and 11, however, which are absent in the latter insect, are mostly visible in *B. severina* ♀. *B. calypso* is noticeable as having the present series particularly well-marked on the underside of the hindwing; in the female it is also well in view on the upper surface. *Pinacopteryx larima*, again, has the series well developed on the hindwing, and recalls some species of *Synchloe* and *Ganoris* by the prominence given to S 8, 10, and 11. In several species of *Belenois*, as for instance *B. teutonia* ♀ and *B. coronea*, the fusion of the spots of series S with one another and with the dark apical and marginal area is almost or quite complete. (See *B. peristhene*, Fig. 14).

The genera *Appias*, *Catophaga*, and *Hiposcritia* present us in many of their members with the same series, more or less developed. In *H. lalage*, for instance, S 1—9 are fairly well marked on the forewing (most distinctly on the underside); while some spots of the series are also in most cases visible on the hindwing. In the greater number of species, however, the series is so fused with the dark apical and marginal area as to be hardly distinguishable (as in *C. zamboanga* ♀), or is altogether obsolete (as in most specimens of *A. nero*). It is noticeable that the spot S 8, to which I have before drawn attention, is usually the last to disappear from the forewing; and that in many cases where S no longer exists as a separately recognizable series, the place of S 8 is indicated by a prominent projection inwards of the fused marginal area (Figs. 9, 10, 11). The underside of the hindwing often retains traces of the submarginal series when the upper surface of one or both wings has entirely lost them (*C. lankapura* ♀ and some specimens of *A. nero*).

In the genus *Delias* the same assemblage of spots meets us again, though scarcely in a very definite form. The well known *D. eucharis* (Fig. 5) shows the series on both surfaces of each wing, the spots being to a great extent merged with one another; the band formed by their fusion is nevertheless quite distinct, and its indentations correspond with the usual disposition of the spots on the wing in those species where they exist in a more discrete condition. The series is also visible in *D. hyparete* (underside); and the same range of markings is present as a sinuous band in the Australian *D. aganippe* (best seen in the female, and on the underside); in less distinct form in *D. harpalyce*, and still recognizable, though now almost completely merged, in the closely allied *D. nigrina*. A comparison of the upper surface of the wings of the last named insects with those of other species of the genus *Delias*, such as *D. belladonna* (Fig. 4), *D. pasithoe*, and *D. thisbe*, serves to suggest the manner in which the submarginal series (in common with other features) may have arisen—namely, as a survival of an original dark ground-colour, which has become broken up, first into irregular bands and finally into spots, by the appearance and gradual enlargement of touches of a lighter colour in the spaces between the nervules. Further reference will be made to this point when other markings, whose history appears to be similar to that of the present series, come under consideration.

Metaporia agathon (Fig. 7) presents the series in much the same condition as *D. eucharis*, the band is, however, somewhat thicker and less defined. It is easy to trace the same feature through many species of the genera *Pontia* and *Huphina*; thus in *P. soracta* it is met with in the hindwing as a series of faintly-developed acute-angled chevrons, pointing outwards (as in *Tatochila*). In the forewing, S 3, 5—9 are easily visible. It is noticeable that S 8 is in this insect exceptionally small; it retains, however, its usual tendency to break the line of the series by advancing further than the others towards the centre of the wing. In *Pontia cratægi* the whole series has vanished; but in *Huphina coronis*, *H. phryne* (Fig. 8) and others, it is well marked; the most persistent spots being, as in other genera, S 6, 8 and 10; and the same general differences between the sexes, in relation to the series, being observable here as in *Synchloe*

and *Ganoris*. Indications of the series, more or less pronounced, can also be seen in *H. timnatha*, *H. aspasia*, *H. judith*, *H. nama*, and other species.

The strong resemblance to *Delias belladonna* borne by *Prioneris thestylis* is very probably due to mimicry, as suggested by Wallace ("Pieridæ of the Indian and Australian Regions," Trans. Ent. Soc. Lond., 3rd series, iv., pp. 309, 383). But from the presence of traces of the submarginal series in other species of *Prioneris* (as in *P. autothisbe* and *P. clemanthe*), it seems likely that it is rather the retention than the origin of the submarginal series in *P. thestylis* that is attributable to this cause. Material for the production of a likeness of *D. belladonna* was no doubt already to hand in the existence of an homologous series of markings in both insects. Other species of *Prioneris*, not having the same reason for keeping close to the original design, have strayed away more or less widely from it.

Mr. Wallace has also pointed out the agreement in some respects between *Delias* and the South American genus *Euterpe* (ibid., p. 344). If, with Mr. Butler, we divide Swainson's genus *Euterpe* into *Pereute*, *Leodonta*, *Catasticta* and *Euterpe* proper, we shall find that while all the normally coloured species of the group are demonstrably linked with one another and with *Delias* by their general system of marking and scheme of coloration, two of the genera (*Pereute* and *Leodonta*) further suggest a near relationship with *Delias* by the peculiarities of their neuration; there being in these instances only three instead of four subcostal nervules in the forewing (Butler, "Revision of the Genera of the Subfamily *Pierinæ*," Cistula Entomologica, vol. i., 1870, pp. 39, 40, etc.). The appearance of several species of this group of genera (notably *Euterpe tereas*) has been profoundly altered by mimicry; but putting aside such forms as these, we shall find no difficulty in tracing a common pattern throughout most of the remaining members of the group. This pattern is not dissimilar from that which characterizes those species of *Delias* which we have seen to be probably the older (*e.g.*, *D. belladonna*, *D. pasithoe* and *D. thisbe*). To this part of the subject I shall return later, at present it will be sufficient to point out the distinct presence of the submarginal series S in such examples as *Catasticta*

nimbice, *C. anaitis*, *C. bithys*, and to a less degree in *Leodonta dysoni* and *L. tellane*. The close resemblance between the remarkable Pierine *Eucheira socialis* and *C. bithys*, in respect of the marking of the upper surface, may warrant us in identifying the corresponding portion of the wing in the former insect with the submarginal row S undoubtedly present in the latter (Figs. 1, 2).

The series S having now been traced through several genera, until it, so to speak, loses itself in such generalised, and apparently primitive forms as those presented by *Delias belladonna*, *Catasticta bithys* and *Eucheira socialis*, it will be advisable to return to the genus *Synchloe*, and seek thereabouts for a new starting-point from which to pursue the same series through its developments in a fresh assemblage of genera which have not at present been noticed. Such a starting-point may be found in a comparison of *S. daplidice* ♀ with the female of almost any species of the genus *Colias*. A short examination will show that the same submarginal series exists in the latter genus. A good species for the purpose is *C. hyale* (Fig. 20), in which both sexes exhibit the series distinctly. The constituent spots broaden out towards the costa and tend to become fused with one another and with the black patch at the apex. This tendency is carried further in many species of *Colias*, particularly in the males, where, as in *C. edusa*, marginal and submarginal markings are fused together into a deep dark border. The females, however, preserve the spots of the submarginal series in a more discrete condition. In most species of *Colias* S is well developed on the under surface, the component spots being usually black on the forewing, and on the hindwing orange or pinkish. In a few species, such as *C. phicomone* and *C. palæno*, the series is obscured or absent. *Meganostoma*, which resembles *Colias* so closely in other respects, shows also the submarginal series on the under surface; usually as a row of somewhat faint pinkish dots, which are clearly identical with S in *Colias*.

Through *Meganostoma* the passage is easy to *Gonepteryx* and *Amynthia*. In *G. rhamni* and *G. cleopatra* no vestige of S is to be seen on the upper surface; on the lower surface, however, of many of the males and most

of the females, it is visible in the hindwing, and near the apex of the forewing, as a series of minute brownish dots; similar to, but as a rule even smaller than, those of *Meganostoma*. *Rhodocera leachiana* and *Amynthia mœrula* show exactly the same feature, the spots being dark brown or black, and a vestige of the series is present in *A. clorinde*. In the closely-allied genus *Dercas*, S is curiously modified into a brown or orange streak passing in an almost straight direction from the apex of the forewing to the anal angle of the hindwing. In *D. wallichii*, S 8 is large and prominent; but the remainder of the series is scarcely visible on the upper surface, though easily recognisable below.

In the genera *Callidryas*, *Catopsilia*, and their allies, the extent to which S is developed varies within wide limits. *Callidryas philea* ♀ has already been noticed as presenting, on the upper surface of the forewing, in many specimens, a complete set from S 1 to S 11 (Fig. 22). In this, as in other species of the genera named, it is usually S 7 and not S 8 that breaks the line by advancing towards the centre of the wing. The series is not usually continued on the upper surface of the hindwing, but both wings show it tolerably well below. S is well developed on the upper surface of *Catopsilia flava* ♀ (Fig. 21), and is visible to a variable extent on both surfaces (except the upper surface of the male) in *C. catilla*, *Aphrissa godartiana*, and others. In some of these insects S on the under surface forms part of the characteristic brown or pinkish mottling of the wing; in others, as the male of *C. phlegeus*, it is almost or quite reduced to the condition of minute pink spots, like those of the genus *Gonepteryx*. It is worth noticing that on the underside of *Phœbis trite*, S takes in the forewing the form of a straight streak, not unlike that in *Dercas lycorias*, leading diagonally across the wing. On the hindwing a similar streak appears, which, however, does not represent S as the apparently corresponding streak in *Dercas* undoubtedly does, but is at least partly developed from another system of spots which will be noticed later. Attentive examination will disclose the existence of traces of the true S between the streak in question and the hind border of the wing.

In *Hebomoia* the series is always at least partly visible on the forewings, and often on the hindwings as well.

The component spots are usually large and distinct, as may be especially well seen in *H. glaucippe* ♀ (Fig. 19). The same insect also shows the series tolerably well on the under surface, where it is in other members of the genus, as a rule, somewhat lost in the general mottling of the wing.

S is often well seen on the underside of species belonging to the genus *Ixias*, where it assumes a condition very like that which obtains in *Colias*. In *I. marianne* it is especially well developed, and the component spots on the hindwing are often furnished with pale centres. Some members of the series are frequently also visible on the upper surface, as in *I. marianne* ♀, where S 6—9 are conspicuous (Fig. 18).

The genera *Teracolus*, Swains., *Idmais*, Boisd., and *Callosune*, Doubl., are united by Mr. Butler as *Teracolus*. In most of the species included under this head, the series now being discussed is distinctly visible, especially in the female and on the under surface. Good examples of the series are furnished by *T. danae* and *T. etrida*. In *T. eucharis* ♂ it has mostly vanished from the upper surface; S 8, however, remains, as in so many other instances, and is, moreover, in this insect often reinforced by the presence of S 13 and 14, which spots have been also seen to persist in our common species of *Ganoris*. The female of *T. regina* possesses S in a well-developed condition on both surfaces, S 10 being especially conspicuous. The same series is visible to a less degree in the female of *T. ione*. The males of both species show indications of S on the lower surface, but none on the upper. The series may also be seen in a well-developed state in *T. hewitsonii* and *T. amata* (Fig. 17).

In *Euchloe* the series has almost disappeared. A relic, however, persists near the apex of the forewing in some species, best seen, perhaps, in *E. tagis*, *E. ausonia*, and *E. hyantis*; while *E. reakirtii* ♀ shows S on the upper side of the forewing very distinctly; S 8 indenting the line as in the genus *Synchloe*. A comparison of the under surface of the hindwing in *E. cardamines* and *E. eupheno* with the somewhat similar system of marking in *S. daplidice* suggests also the probability that part of the green mottling in *Euchloe* represents the submarginal series. The same series is certainly visible on the upper surface of the hindwing in some specimens of *E. lucilla* ♀.

Certain species of *Nepheronia*—for example, *N. jobæa* ♀ and *N. valeria* ♀—show the series S in a form that strongly recalls the condition of the same series in *Metaporia agathon*. In both *Nepheronia* and *Eronia*, however, S is very apt to be merged, especially on the upper surface, with the dark marginal area. The female of *E. leda* (Fig. 23) shows the first few spots of the series on the upper side of the forewing in a condition resembling that in some species of *Callidryas*, which resemblance applies also to the lower surface, where S occurs in a modified form on both wings, traces of the same series being likewise visible in the male.

Summary.—Most of the members of the subfamily *Pierinæ* possess, in a greater or less state of development, a submarginal series of dark spots. The genera *Synchloe, Belenois, Tatochila*, and some species of *Colias*, amongst others, present the series in a fair state of completeness. In other members of *Colias*, and in several genera such as *Ixias, Hebomoia*, and *Teracolus*, the series is often less distinguishable, owing either to fusion of its constituent spots with each other and with the dark marginal area, or to suppression of some of their number. Relics of the series remain in *Ganoris, Euchloe*, and other genera, being especially persistent in the female sex; in *Gonepteryx, Dercas, Callidryas, Phœbis, Catopsilia*, and other allied genera, the series often undergoes curious modifications. The aspect of the series in such genera as *Pontia, Huphina, Metaporia*, and *Nepheronia*, suggests its development from portions of the original ground-colour left (by the formation and subsequent fusion of lighter patches in a dark or dusky area) as a dark band following the contour of the wing; and, finally, by an extension of the process, as a submarginal chain of spots. The possibility of such a mode of origin is well illustrated by the condition of the wings in many species of the Eastern genera *Prioneris* and *Delias*, and the Western *Leodonta, Catasticta*, and *Eucheira*.

2. *The dark marginal area or spots.*

In nearly all our common *Pierinæ* we find a dark patch at the apex of the forewing; better marked, as a rule, in the females than in the males. In *G. brassicæ*

it is large and crescent-shaped, extending for some distance along both costa and outer margin of the wing. In *G. rapæ* ♀ it is not as a rule prolonged very far on the outer margin, but it still reaches some way along the costa. In the male of the same insect it is generally small, and confined to the actual region of the tip. In neither of these species is there much indication of resolution, except that in most specimens of *G. brassicæ*, especially in the females, the hinder arm of the dark crescent shows an irregularity due to the massing of black scales about the marginal terminations of the nervules. But in *G. napi* (Fig. 16) resolution is generally well marked; and it becomes evident that the dark crescentic or triangular area of the tip is really formed by the fusion of the anterior members of the series S, which we have just been considering, with another series, which may be called M, occupying the actual margin of the wing, and consisting, in its fully resolved condition, of a row of dark spots, each of which is traversed by the peripheral portion of one of the nervules. It is noticeable that in this species the black marginal spots are often found extended, especially in the female, in the form of a powdering of dark scales along the course of the nervules towards the base of the wing.

Turning to *S. daplidice* (Fig. 15), we find the constituent elements of the apical patch still better shown than in *G. napi*. The marginal and submarginal series are always distinct, being separated from one another by portions of the general white colour of the wing, which take the form of a row of white spots on the dark apex, usually four in number. Either of these two species serves well to illustrate an important difference between the spots of the two series, S and M. The spots of the former series occupy, as we have seen, the interspaces between nervules; and when fusion between adjacent members of the series takes place, it does so by an extension of dark scales across a nervule. On the other hand, each of the spots of the latter series is centred, not in an interspace, but around the peripheral portion of a nervule or nervure. Thus the spots of the two series tend to alternate with one another, though this effect is to some extent interfered with by the frequent fusion of some of the spots with others of the same

series. It is further noticeable that in both of these insects the marginal series M is usually continued in the form of a row of dots smaller than those helping to constitute the apical patch, but still distinct, along the outer border of both fore and hindwing. In *S. daplidice* ♀ (Fig. 15), the submarginal series being also distinctly present on the hindwing, the alternate arrangement of the two series is in this situation very apparent. The constituent spots of series M may be numbered for convenience, in the forewing 1—11, in the hindwing 12—20, one being counted for each nervure or nervule that reaches the margin; and the same allowance may be made as was suggested in the case of S for the occasional suppression of a fourth or addition of a fifth subcostal nervule (see p. 255).

Many examples of the occurrence of this marginal series can be found among the near allies of the species just named, and in all of them there is a tendency towards the formation of a dark apical patch by the union near the tip of the forewing with the anterior members of the submarginal group S. In *G. gliciria* many members of the series are usually present, often tending in the females to form by fusion a broad marginal band in both fore and hindwing. Other species of the genus *Synchloe* besides *S. daplidice* present M in a fairly well-developed condition. It is usually conspicuous in the female *S. callidice*, *S. protodice* and *S. hellica*, and to a less extent in the males of the same insects; where it clings longest, as in the common species of *Ganoris*, to the region of the tip. *Tatochila autodice* and *T. theodice* show M in very nearly the same condition as the species of *Synchloe* last named.

Turning to the genus *Colias*, we find that the marginal series has undergone some modification. In the males it is often completely fused with the submarginal series, the two together forming a broad outer band to the wing, as in *C. edusa* ♂. The same may also take place in the female, as in *C. palæno*; but in most cases the two series, S and M, are in the female more or less distinct, being marked off from one another by areas of ground colour which take the form of a row of light-coloured spots, not unlike those present in many species of *Synchloe* (see p. 263). In some instances, as in *C. hyale* and *C. phicomone*, this description applies also

to the males. Most species show a strong tendency for the spots S 8 and M 8—9, and, in a less degree, S 10 and M 10—11, to become fused with one another by the obliteration of the separating patches of pale ground colour. The individual members of series M are usually more distinct from one another on the hind than on the forewing. Not infrequently they are fused into a complete band in both. On the lower surface M is in this genus rarely if ever visible; thus offering a strong contrast to S.

In *Meganostoma* the fusion of M with S is usually complete on the forewing; the females, however, of some species show traces of a separation; a few patches of the yellow ground-colour, like those in the females of many species of *Colias*, appearing in the midst of the dark border. In some forms, as *M. philippa* ♀, these light patches become much enlarged, and the two series S and M are as distinct from one another as in any species of *Colias*. *M. cesonia* usually shows the spots well on the upper surface of the hindwing; and in most species of this genus, M is often visible beneath as a row of minute pinkish dots on the terminations of the nervules at the margin.

In *Gonepteryx*, *Rhodocera*, *Amynthia*, and *Dercas*, the series is not as a rule strongly developed. *G. rhamni* usually shows on both surfaces a row of marginal dots, dark red or brown above and pinker beneath, at the outer extremities of the nervules, which are undoubtedly relics of M. These are best marked at the tip of the forewing, where they often tend to run into a thin continuous marginal line, and are generally more apparent in the female. The apical band is more strongly accentuated in *Rhodocera leachiana*, especially in the female, in which sex also M is often found on the hindwing in a fairly developed condition. Traces only of the series are visible in the species of *Amynthia*; but in *Dercas* M is reinforced by the anterior portion of S, and helps with it to form a conspicuous dark area at the region of the tip.

The condition of M in *Hebomoia* needs no special remark, except that on the under surface its separate existence appears to be sacrificed to the exigencies of the protective pattern.

In *Callidryas*, *Metura*, *Phœbis*, *Aphrissa*, and *Catop-*

silia, the development of M varies. Most of the species, however, show the usual tendency of M to expand into an apical patch, either with or without reinforcement from S. The members of the series are generally reduced on the lower surface of the hindwing to a row of marginal dots; and the great characteristic of the present series, namely that it belongs to the nervules, and not, like the former one, to the interspaces, is kept up throughout. On the upper surface of *Catopsilia flava* ♀ (Fig. 21), M and S are both well developed, and their relation to one another closely resembles that which obtains in *Colias*.

The same series is often present in the genera *Ixias* and *Teracolus;* being, as usual, most constant in the females, and most prominent on the upper surface. It appears occasionally as a chain of spots, as in the hindwing of many specimens of *T. ione* ♀, and some of *T. regina*, but more often as a simple marginal band, as in *I. marianne* (Fig. 18). This band may be completely fused with S, as in the hindwing of *T. phisadia*, or partially so, as in *T. amata*. A plain marginal band, in the forewing expanding at the tip and more or less indented opposite the branching of the median nervure, in the hindwing sometimes breaking into a chain of spots, is also the usual condition of M in the genus *Terias*.

In *Nepheronia* and *Eronia* M is generally present as a well-developed marginal band sometimes more or less fused with S, and often sending dark prolongations inwards along the course of the nervules. In some species, however, as *N. thalassina* and *E. leda*, it is mostly confined to the apical region; in the latter indeed it is absent from the hindwing of the male altogether, and barely visible on that of the female (Fig. 23). The series in *Euchloe* is generally recognizable as a row of dots, sometimes fused at the apex with the anterior members of S; but often, as in *E. tagis* and *E. ausonia*, preserving its independent existence.

The condition of M in the genera *Metaporia* and *Huphina* recalls that in *Nepheronia;* the constituent spots being generally fused into a marginal band from which dark offshoots run inwards, accompanying the course of the nervules. A similar description will apply to *Pontia*, though in this genus the dark markings are often greatly

reduced. *P. soracta*, however, shows M with sufficient distinctness; and even in *P. cratægi* M itself is in some instances visible, while the dark prolongations along the course of the nervules is a well-known and conspicuous feature.

Delias and *Prioneris* help to show us what is in all probability the earliest condition of the present as well as of the former series. The upper surface of both fore and hindwing in the female of *D. eucharis* presents once more the familiar pattern of *Metaporia agathon* and *Nepheronia gæa* ♀. It has already been pointed out that there is an easy passage from this system of marking to that which we find in *D. belladonna*, *D. pasithoe*, and several other species; while the same features are undoubtedly visible with but slight modification in the American genera *Euterpe*, *Catasticta*, *Leodonta*, and *Eucheira* (see p. 258). A comparison of the insects just named, to which may be added *Prioneris thestylis* and other species of the same genus, can hardly fail to suggest the probability of the origin of both M and S as portions of the original dark ground-colour marked off from one another with gradually increasing distinctness by the appearance, enlargement, and confluence of whitish patches in the interspaces between nervules. The alternate character of the two series S and M, when broken up into spots, is seen to be a consequence of the shape and position of the original dusky white touches that first bring them into view. These touches may be seen for example in *D. belladonna* (Fig. 4) to be divisible into two sets, which we may call marginal and basal, both occupying the central areas of the interspaces. Between the two sets is included the portion of ground colour corresponding to S, the constituent spots of which, when isolated, will necessarily have their centres in the interspaces. But the marginal set of light marks tends to reach by tapering extremities to the edge of the wing (see Fig. 5); so that the interposed marginal patches of unaltered ground colour, forming the first beginnings of M, are of necessity focussed round points in the nervules an d not in the interspaces. And when in consequence of the further development and fusion of the white or pale markings, the marginal relics of dark ground colour become reduced to a row of isolated dark spots, these spots are, as we have already seen in *S. daplidice* (p. 263)

and other cases, always traversed by the peripheral portion of a nervule or nervure. This fact is well exemplified by *M. agathina*, *M. poppea*, and several other species of *Mylothris* (Fig. 12).

The invasion of white, which is already considerable in *D. eucharis* ♀, becomes still more predominant in the male of the same insect, where, however, the original ground-colour still persists, not only in the series S and M, but also in the form of the dark streaks accompanying the nervures and nervules, a feature which we have seen to be common in many other genera, especially *Pontia*, *Huphina*, *Metaporia*, and *Nepheronia*.

Without leaving the genus *Delias* we can find several examples where the intrusive white has ousted the whole of the original ground-colour, except at the margins and apex. This is the case for instance in *D. descombesii* ♂, *D. agostina* ♂, *D. cœneus* ♂, and *D. momea*. In most of these species the dark marginal area is plainly composed of S and M in a more or less complete state of fusion, and it is noticeable here as elsewhere that the female almost invariably retains a larger proportion of the original ground-colour than the male.

Many species of *Belenois* resemble the last mentioned species of *Delias* in the tendency towards fusion of the marginal and submarginal series. *B. peristhene* (Fig. 14) is exceedingly like *D. momea* in this respect, and in *B. teutonia* ♀ and *B. coronea* the fusion is still more complete. But in very many species of *Belenois* and *Pinacopteryx*, S and M are plainly distinguishable from one another; and in some, as in *B. calypso* (as also in *Pinacopteryx capricornus*), the resolution of both into a row of dots is complete. The formation of a series of rings along the margin of the hindwing (as in *Synchloe callidice* ♀, *S. protodice* ♀, etc.), by the union of the horns of the crescents or chevrons belonging to series S with the spots of series M, is a noticeable feature on both surfaces of many specimens of *B. mesentina* ♂ (see Fig. 13); and the identity of the whole arrangement of the submarginal and marginal series in *Belenois* with that in *Synchloe* becomes perfectly evident on a comparison of *B. mesentina* with *S. johnstonii* or *S. hellica*.

In *Appias* the two series when present are not sharply marked off from one another. In some species, however, S has almost or quite disappeared, and M may persist

alone as a marginal band, showing more or less tendency towards resolution (*Appias lyncida* ♂, *A. celestina* ♂, etc.).

Summary.—The present, like the preceding series, is thus seen to be a relic of the original dark ground-colour. It is intercepted between the margin of the wing and a series of pale touches (best seen in certain species of *Delias* and *Catasticta*) that making their appearance in the submarginal region of the interspaces, more or less isolate, indent and divide up the dark marginal area. It may eventually disappear altogether (as in some specimens of *G. rapæ* ♂), but usually persists on the forewing, at least, in the region of the apex. When present, it shows great variation in the extent to which it is resolved into separate spots, and also in the amount of fusion it undergoes with the neighbouring series S. As a general rule it is, like the last-named series, more constantly present in the female sex, and more completely resolved in the male.

3. *The light series between* 1 *and* 2.

The region of pale ground-colour included between the two dark-coloured series S and M, becomes of necessity more sharply defined and circumscribed as the constituents of each dark series become fused together into bands instead of remaining as rows of spots. The tendency so often seen of the two dark series to become partially fused with one another, by the extension between them of dark lines following the course of the nervules, leads, when carried far enough, to the splitting up of the included pale area into a series of pale spots, which sometimes attain a very distinct and definite character, especially at the apex of the forewing. These pale spots have already been incidentally noticed during the discussion of the two series between which they lie; it will not be necessary to do more in this place than to suggest that, for the purpose of separate reference, the letter I should be taken to represent the whole series, the possible constituents being numbered 1—20, in correspondence with the dark spots of series S which bound them on the inner aspect. (See Figs. 1, 2, 5, 21, etc.)

4. *The discoidal spots.*

In none of our three common species of *Ganoris* does

there exist a true discoidal spot. The nearest approach is to be found in *G. napi*, where the disco-cellulars of the forewing, together with the other nervules, are in many specimens accompanied by a sprinkling of black scales; which in some instances are sufficiently numerous in this particular region to give almost the appearance of a black discoidal spot or patch. This may be best seen in specimens of *G. bryoniæ*, but dusky specimens of the ordinary *G. napi* will sometimes show the tendency almost equally well. The same tendency is carried a little further in *Tatochila autodice*, while *T. theodice* shows the corresponding marks in a condition of strong development, with a slight indication of a similar feature on the hindwing as well. Passing to the genus *Synchloe*, we find the discoidal spot invariably present, at least in the forewing; and in most species large and distinct, especially in the females. *S. daplidice* (Fig. 15) has the spot well developed on both surfaces; on the lower surface it is more or less shaded with green. The same is the case with the somewhat smaller discoidal spot in *S. callidice*. Another example of a large and conspicuous discoidal spot is furnished by *S. hellica*.

In *Colias*, a discoidal spot is nearly always present on each surface of both fore and hindwings. On the upper surface of the latter it is sometimes independently present and sometimes only shows through from beneath; but it is seldom absent altogether. The spot on the forewing is in this genus, as in *Synchloe*, usually dark brown or black. It may be ringed or pupilled with orange; in the former case the orange is of a deeper shade than the general ground-colour. Examples of this may be seen in *C. meadii*, *C. cunninghamii*, and others. In *C. fieldii* and *C. edusina* the discoidal spot in the forewing is unusually large; in no species of *Colias*, however, does it overpass the boundaries of the subcostal nervure in front and the third median nervule behind. It may be very small, as in *C. barbara*; or entirely absent, as in some specimens of *C. palæno* and *C. pelidne*. On the lower surface it is often centred with white or silver. On the upper surface of the hindwing, the spot when present is not dark, but varies in different species from the palest yellow to a full orange. It is distinguished from the general surface of the wing either by its different shade of yellow or orange (as in *C. hyale*)

or by its freedom from admixture with the darker scales that often give the hindwing in this genus a comparatively dusky appearance (as in some specimens of *C. edusa*). In many species a small companion is visible in the interspace between the second subcostal and discoidal nervure. On the under surface the discoidal spot is much more distinct. Its centre is silvery white, and it is usually encircled with a brown or orange ring, which in some species is sharply marked off both internally and externally by thin marginal lines of a darker colour. The companion reproduces the discoidal spot on a smaller scale. It always occupies an interspace, whereas the chief discoidal spot is situated upon the second disco-cellular nervule. (Fig. 20, D 4.)

No doubt is likely to arise as to the identity of the discoidal spot in *Synchloe* with that in *Colias* so far as the forewing is concerned. The chief difference between them is that in the former genus the spot is less sharply defined and less regular in outline; moreover in *Synchloe* it frequently reaches forward to the costa, and it may extend backward to the space between the first and second median nervule; whereas in *Colias*, as we have seen, it does not pass the limits set by the subcostal nervure and the third median nervule. But there can be no reasonable question that the spots are homologous in the two cases; and a comparison of the two genera further suggests the probability that in *Synchloe* we have an older, in *Colias* a newer and more specialised form of the marking. This conclusion accords with what has been already said about the marginal and submarginal series of markings, which in *Colias*, especially in the males, have departed somewhat further from the original type than in *Synchloe*; and it will be seen to receive further confirmation from what is to follow. With regard to the discoidal spot on the hindwing, although it is perhaps not at first sight clear that the markings in the two genera are really homologous, it is nevertheless quite possible, on an attentive examination of allied forms, to trace the steps by which the passage from one to the other is effected. In the hindwing of many species of *Synchloe* there is no indication of a discoidal spot at all; in others, however, a definite aggregation of black scales is visible about the disco-cellular nervules. In some species, such as *S. protodice* ♀,

the nervules, though surrounded with black scales, are themselves covered with white, or (on the underside) pale yellow scales; a light-coloured centre being thus provided for the dark discoidal patch. In the genus *Tatochila* this light-coloured centre acquires greater importance. On the under surface of *T. autodice* the white scales are seen not only covering the disco-cellular nervules, but also intruding some way upon the yellow of the general surface; in this species, however, the pale patch thus formed has no dark border. But there can be little doubt, on a comparison of *T. autodice* with *Colias palæno*, that the whitish area surrounding the second disco-cellular nervule in the one is homologous with the silvery patch in the corresponding region of the other; while the identity of the discoidal marks in *Tatochila* with those in *Synchloe*, and of the same marks in *C. palæno* with those in other species of *Colias*, is a matter of certainty. The brown ring surrounding the silvery pupil on the under surface of most species of *Colias* is indicated in *C. palæno*, where its general appearance points to the probability of its origin from the dark scales that have already been noticed as gathering about the region of the disco-cellular nervules in *Synchloe*. In *C. palæno* itself, however, the central pale patch (as in *Tatochila*) becomes far more prominent than the surrounding dark border. An examination of the discoidal spot on the underside of the hindwing in *Gonepteryx rhamni* ♀ and *Amynthia mærula* will disclose the same general arrangement of a pale area traversed by the second disco-cellular nervule, and surrounded by a ring of darker scales, that we have already seen to be characteristic of the spot in other genera. In these insects, however, as in *Rhodocera leachiana*, the spots, though clearly identical with those in *Colias*, are in a lower state of development and specialization. Turning again to the discoidal spots on the forewing, we may at first sight hesitate to identify the bright orange spots in *G. rhamni* or *G. cleopatra* with the black spots or patches in *Synchloe* and *Colias*. But in *Amynthia clorinde* we have what is unmistakably an intermediate form of the spot, in which the vivid orange of the one closely encircles the deep brown or black of the other, and from which either the *Gonepteryx* or *Colias* type of spot might be easily derived. Much the same is the case with *R. leachiana*;

but in this insect the black markedly predominates. The discoidal spot in the forewing of *R. leachiana* is also noticeable as having a small companion, of similar character but with a greater proportion of orange, in the root of the interspace between the subcostal and the first discoidal nervure.

The discoidal spots in *Dercas*, when present, correspond closely with those in the genera just named. The spot on the forewing of *D. lycorias* is like that in *G. rhamni*; it is, however, less compact, and surrounds both disco-cellular nervules instead of the second only, as in the latter insect. The spot on the upper surface of the hindwing is scarcely visible, but those on both wings beneath nearly resemble the corresponding marks in *R. leachiana*. On the underside of *D. wallichii* the marks are of the same character, but reduced in size; from the upper surface they are almost or quite absent.

In *Meganostoma* the discoidal spots, both above and beneath, so closely correspond with those in *Colias* as to call for no special remark. In *Callidryas*, *Metura*, *Phœbis*, *Aphrissa*, and *Catopsilia*, they present also the same general appearance. On the upper surface of the hindwing, the discoidal spot is seen as a rule faintly or not at all; but on the forewing there is often a well-marked dark patch, enclosing either the second disco-cellular, as usually in *Catopsilia thauruma* and *C. catilla* ♀, or both disco-cellulars, as in *Aphrissa godartiana* ♀. On the underside the form of a silvery circular patch, surrounded by a pinkish or brownish ring, is almost universally kept up. There is in some species (as in *Callidryas philea*) a tendency for the discoidal spot in the forewing to divide into two parts, one for each disco-cellular nervule; while in the hindwing the small companion which has been already noticed in *Colias* is nearly always present in the interspace between the discoidal and subcostal nervures. One or two species (as *C. florella* ♀) possess a second companion within the cell. The present series, when fully resolved, seems thus to consist of five spots, two belonging to the two disco-cellular nervules in the forewing, the third belonging to the interspace between the subcostal and discoidal nervures in the hindwing, the fourth to the second disco-cellular nervule, and the fifth to the discoidal cell,

also in the hindwing. I propose to designate the system as D 1—5.*

The last-named genera exhibit a good deal of variation in the size of the constituent spots of D, and also in the breadth of the encircling darker ring. In *C. catilla* ♀, the latter, spreading widely out from the silver centres, and being reinforced in the hindwing by a similar development from certain of the spots of series S, forms a conspicuous dark red patch on the under surface of both primaries and secondaries. A similar tendency is seen in many specimens of *Callidryas thalestris* and other members of that genus. In all these cases the border of the discoidal spots on the under surface is assimilated in colour to the general character of the darker mottlings that form the prevailing feature of the wing-pattern. It is interesting to observe, in the case of *Phœbis trite*, that the straight diagonal streak already referred to (p. 260) as crossing the under surface of the hindwing is made up of elements belonging to both series S and D, as follows: The part between the two subcostal nervules is S 14; that between the subcostal and discoidal is D 3; the next, where the streak intersects the second disco-cellular, is D 4; it then skips a space, and reappears between the median and submedian nervures as S 19. That the homology of the different parts of this line has been correctly stated will be evident from a comparison of *P. trite* with *C. eubule* and *C. thalestris*, in which species the elements of the streak are visible in a separate condition. It is in *P. trite* particularly worthy of note that in those interspaces where D 3 and 4 form part of the streak, the corresponding members of S, viz., S 15, 16, and 17 (which are not wanted for this purpose), are visible well to the outer side of the streak; whereas in the other interspaces there are no marks between the streak and the margin, the members of S having been, so to speak, used up for another purpose, and having thus caused an apparent interruption of the usual submarginal pattern. In the interspace between the first and second median

* This use of D is open to the objection that the same letter has also been used for an entirely different set of markings in the Nymphalidæ (see Trans. Ent. Soc. Lond., 1890, p. 91). But I do not think that this circumstance is likely to give rise to any practical difficulty.

nervules, S 18 appears as a submarginal spot of the usual kind. Now, inasmuch as no member of series D ever occupies this interspace, there is no material at hand for continuing the streak; and, carrying the eye up to the apex of the interspace, where the streak should cross, we find it, in fact, deficient at that place.* This may seem a small point, but it is of interest as illustrating the absence of anything that might be called violent or arbitrary in the evolution of these various patterns, in which, indeed, the closer the examination the more difficult it is to find anything effected *per saltum*.

In *Ixias* the condition is again much the same as in *Colias*; the discoidal spot of the forewing, however, is often united on the upper surface with a dark band running across the wing from the costa to the anal angle. A similar feature occurs in *Hebomoia glaucippe* (Fig. 19) and other species of the same genus. On the lower surface the discoidal spot varies considerably in size, and in a few cases (as sometimes in *I. marianne*) may be absent altogether. When it is large, as in other specimens of *I. marianne*, it is frequently centred with white. In the hindwing the series is absent from the upper surface, and represented below only by D 4, which may also be white-centred, or may exist as a simple black dot of varying size.

In *Teracolus*, D is usually well marked. In some species, such as *T. vesta*, *T. hewitsonii*, and *T. puellaris*, it occurs on the forewing as a conspicuous black patch covering both disco-cellular nervules, and usually merged anteriorly in a dark or dusky band which extends along the costal border. In other species, as *T. evanthe*, *T. ione*, *T. regina*, etc., it takes the form of a circumscribed black spot, sometimes minute or absent. On the lower surface, the scales on and surrounding the disco-cellular nervules are often whitish, thus giving D a pale centre. D in the hindwing, when present, is usually small; on the underside of some species, as *T. danae*, *T. evippe*, and *T. omphale*, it is centred or shaded with orange;—this tint belonging primarily to the disco-cellular nervules, and spreading more or less widely from them.

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* As above noted (p. 260), the corresponding streak in the *forewing* of *P. trite*, and the somewhat similar feature on both wings of *Dercas lycorias*, are entirely formed out of series S.

In *Terias* and *Sphænogona*, D is constantly absent from the upper surface, but is usually visible below, where it may appear as a small black dot or pair of dots in each wing (*T. lisa*), or as a group of more or less regular narrow-bordered rings (*T. hecabe* and *T. floricola*), or in various intermediate forms (*T. deva* and *S. gratiosa*). The transition from the condition of D in *Colias* to that in *Terias* is well indicated by *Xanthidia nicippe*, most specimens of which correspond pretty closely in the markings of the lower surface with the latter genus; while the upper surface of the forewing bears a discoidal spot much like that in some species of *Colias*. In the closely allied genus *Pyrisitia*, D has altogether disappeared (see *P. proterpia*).

The genus *Euchloe* shows the discoidal spot on the forewing in a well-marked condition (Fig. 24). It may exist as a distinct spot, as in *E. cardamines*, usually larger in the female; or as a more or less quadrangular patch reaching up to the costa, as in *E. lucilla*. On the underside it is often white-centred, as in *E. belemia* and others. On the hindwing, D is in many species of *Euchloe* not visible at all. In some, however, it appears as a small, at times very minute, patch of black scales surrounding the second disco-cellular nervule (some specimens of *E. genutia* and *E. cardamines*); in others, as *E. charlonia* and *E. lucilla*, it takes the form, on the under surface, of a pale circular patch, closely resembling D 4 of *Colias palæno* in the same situation.

D in *Belenois* is usually well marked on the forewing, as a rule enclosing both disco-cellulars, and often prolonged anteriorly to join the outer extremity of a dark costal band; this is especially the case in the female, and on the under surface in the male, as in *B. mesentina*, *B. teutonia*, *B. calypso*, etc. The spot is sometimes small and quite distinct, as in *B. creona*, D 1 being absent; sometimes, on the other hand, it is large and almost or quite merged in the general dark field of the outer portion of the wing, as in *B. coronea*. In the hindwing there may be no discoidal mark at all, as in *B. creona*; or all the nervures may be covered with dark scales (as generally on the under surface of *B. mesentina*), the disco-cellular nervules not being specially distinguished; or there may be a definite discoidal spot, composed of D 4, as in *B. mesentina* ♀, upper surface;

and in *B. calypso,* under surface of both sexes and upper surface of female.

In *Appias* and *Catophaga* a discoidal spot can scarcely be said to exist; but in *Hiposcritia* and *Pieris* various members of the series D are often well marked. *H. lalage* ♂ (Fig. 11) has a conspicuous discoidal spot on both surfaces of the forewing, formed by D 2; and on the under surface of the hindwing there appears a minute representative of D 4. In *H. pandione,* D 1 and 2 compose a large spot which joins the dark costal band; while on the under surface of the hindwing, D 4 is sometimes indicated by a paling of the first disco-cellular nervule and the immediately surrounding area. In *Pieris* the forewing often shows a conspicuous discoidal spot, formed by D 1 and 2 or by D 2 alone; the hindwing as a rule possessing only a small dark representative of D 4 on the under surface, which in *P. buniæ* merely touches the second disco-cellular, but in *P. pylotis* encloses it.

In *Pontia* and *Huphina* (Fig. 8), D in the forewing appears generally as a mere darkening of the wing in the region of the disco-cellular nervules, more pronounced than the darkening of other nervures which is common in these genera, but not forming a definite spot. In the hindwing it is much less distinguishable or even absent (*P. cratægi, P. soracta, H. phryne, H. timnatha,* etc.). In *Metaporia agathon* (Fig. 7) the same darkening of the disco-cellular area occurs, which in *M. phryxe* takes the form of a definite and conspicuous patch. A like condition is seen in *N. gœa,* and other species of *Nepheronia.*

The correspondence in pattern of the genera *Delias* and *Prioneris* with those just discussed, already referred to on p. 267, applies to the present as well as to other features in the marking. *Delias,* moreover, shows in many species that paling of the disco-cellular nervules themselves, and sometimes of the immediately surrounding area in the midst of the dark discoidal patch, which we have seen to occur in *Synchloe* and other genera, and which in *Colias, Ixias,* and their allies leads to remarkable modifications in the general appearance of the discoidal spots (see *Delias aganippe, D. descombesi, D. crithoe,* etc.). In *D. belisama* ♀, the nervules remain dark, though there is a surrounding pale area.

Nothing special needs to be said about the genera *Euterpe, Catasticta, Leodonta,* and *Eucheira.* Their

general correspondence in pattern with the old-world genera last named, which has been already referred to, involves a similar condition of the present series D. In none of them does any member of D assume the condition of a definite circumscribed spot; but in nearly all, the series exists as a portion of the original dark ground colour between the touches of intrusive white or yellow. In *C. toca*, D on the underside of the hindwing consists of an irregular dark ring with a yellow centre traversed by the disco-cellular nervules, this representing an early condition of the homologous ocellus in *Colias*.

Summary.—This series also, like those already treated of, represents a local survival of the original dark ground-colour. Appearing in the first place as an ill-defined accumulation of dark scales around the disco-cellular nervules, it takes the form of definite spots as the invasion of white or other pale ground tint progresses. As in the case of the other series, resolution is generally best marked in the males; the females showing a greater tendency to adhere to the ancestral condition. When fully resolved, the series consists of five spots, two for the disco-cellular nervules in the forewing, and one for the second disco-cellular in the hindwing, with two extra spots, also in the hindwing. In many instances the disco-cellular nervules, with a varying amount of neighbouring ground-substance, may appear as pale streaks or patches in the midst of the primitive agglomeration of dark scales; and in the further development of the pattern it may happen that either the pale or the dark markings alone persist; or both may be retained and worked up as in species of *Colias*, *Callidryas*, *Ixias*, etc., into a system of more or less elaborate ocelli.

5. *The markings on the underside of the hindwing.*

a. The yellow precostal streak.—A constant feature in our common species of whites is a deep yellow or orange streak which occupies the margin of the precostal space on the underside of the hindwing, and is clearly distinguishable from the pale yellow of the general ground-colour. This yellow precostal streak is conspicuous in other species of *Ganoris*, as *G. gliciria*, and may also be seen in *S. daplidice*, *S. hellica*, and many other members of the genus *Synchloe*. It is, I believe, never found in *Pontia cratægi*; in the closely allied *P. hippia* and *P.*

soracta, however, it is well marked. *Metaporia agathon* and *M. phryxe*, which resemble the last-named species in other respects, also show a deep yellow mark in the same situation; but in this instance it occurs only as a spot bounded outwardly by the precostal nervure, and is not prolonged as a streak along the costa.* Many genera present this mark in much the same condition as the species of *Ganoris* first referred to; of which good examples may be seen in *Nepheronia thalassina*, *N. argia*, the curious *Herpœnia eriphia*, *Pinacopteryx pigea* and *P. capricornus*, *Mylothris chloris* and *M. agathina* (deep orange in these), *Tatochila theodice*, *Glutophrissa margarita*, *Appias zelmira*, *Phrissura sylvia*, *Daptonura lycimnia*, *Teracolus ione*, *T. regina*, *T. eris*, etc.

Looking back to *Synchloe hellica*, we find that the yellow precostal streak forms in that insect only one of a series of yellow marks, one or two of which partially occupy each interspace. A similar condition obtains in many species of *Belenois*; see for instance *B. mesentina* and *B. teutonia*. On the underside of the hindwing in these species, the dark lines following the course of the nervures, and the dark markings belonging to the various series above described, are laid down upon a ground colour which is usually white or pale yellow, but which in many specimens is relieved here and there by streaks and touches of a deeper yellow or orange. One of these streaks occupies the costa, and is plainly identical with the yellow precostal streak in *Synchloe*, *Ganoris*, and the other genera named. Although in the species of *Belenois* just referred to, as in several others, this streak is easily seen to form but one member of a series, it is nevertheless more constant and persistent than any of its companions. This is evident in those not uncommon specimens of *B. mesentina*† in which the general ground colour on the underside of the hindwing takes on so deep a yellow tinge as to approach that of the yellow streaks and touches. In these cases all or some of the latter set of markings may cease to be separately recognizable; the precostal streak, however, is always the last to disappear. In certain species of the

* A specimen of *M. agathon* in Coll. Brit. Mus. has, however, a few orange scales in the *outer* division of the precostal space.

† *I.e.*, the form known as *B. auriginea*.

present genus, as *B. gidica*, the ground colour remains pale; but the precostal streak is the only member of its series present. In others again, as *B. coronea*, the black spots of S exist in a state of enlargement and fusion, while the orange touches occupy nearly the whole of the spaces that are left. The light spots of series I (see p. 269) between S and M, which in *B. teutonia* are only touched with orange, are entirely of that colour in most specimens of *B. coronea*. In *B. peristhene* the amount of light ground colour is smaller still, but the orange costal streak and orange series I are present as in *B. coronea*. Both of these insects, *B. peristhene* in especial, suggest at once a comparison with certain members of the genus *Delias*, particularly *D. nysa* and *D. momea*. In these two species the yellow precostal streak and the yellow or orange series I are unmistakably present. In *D. nysa*, as in *B. peristhene*, these constitute the only relief to the general dark colour of the wing; while in *D. momea* S is partially defined by the presence of pale touches on its inner aspect in addition to the spots of series I along its outer margin.

While the species named suggest a passage in respect of this pattern of the underside of the hindwing between *Belenois* and *Delias*, there is not wanting evidence of the same import in the case of other species in which the blackening of the hindwing is a less conspicuous feature. On the underside of *D. belladonna* we cannot fail to recognize the counterpart of such a hindwing as that of *B. teutonia*; the dark and light areas occupy with slight modification the same relative positions, and the same spaces of pale ground-colour that are in *B. teutonia* touched up with deep yellow, are wholly or partially of the like colour in *D. belladonna*; among these, of course, being the precostal margin. The basal portion of the hindwing in such species as *D. eucharis* and *D. hyparete* shows a more general yellow tinge than in *D. belladonna*; but in both of these, as in other allied species, the deeper-coloured precostal streak is perfectly recognizable. In very many species of *Delias* we meet with a new feature, much of the ordinary yellow being displaced by a brilliant red; but the former colour still displays a tendency to cling to the region of the precostal space, as may be seen in *D. thisbe*; where, however, the precostal yellow hardly reaches further outwards than the pre-

costal nervure. In the very similar *D. pasithoe* it has been driven even from this position.

Prioneris exhibits a condition very similar to that of *Delias*. The underside of *P. thestylis* closely corresponds with that of *D. belladonna*, and the resemblance applies to the precostal streak no less than to other features. In some species of *Prioneris*, as *C. clemanthe* and *P. autothisbe*, the precostal yellow is again approached, and sometimes dislodged, by a greater or less amount of bright red, as in *D. pasithoe*, *D. thisbe*, *D. crithoe*, and other members of the former genus.

Leaving the red patches and other features of the pattern of this region in *Delias* and *Prioneris* for discussion at a later stage, we may pass on to the American genera *Euterpe*, *Pereute*, *Leodonta*, and *Catasticta*. In the two last-named the arrangement of light and dark markings corresponds generally with that in *Delias* and *Belenois*, and similar touches of deep yellow are mostly present in the same relative positions. One of these, usually to be seen on the costal margin, is clearly homologous with the precostal streak in the insects already referred to; in many specimens of *C. nimbice*, *C. semiramis*, *C. toca*, and others, it bears very much the same appearance as in the old-world genera above mentioned. It may be noticed in passing that in many instances, such as *L. zenobia*, *L. dysoni*, and *C. anaitis*, the yellow precostal streak is found sharing the precostal space with a greater or smaller amount of brilliant red, as we have seen to be often the case in *Delias* and *Prioneris*. The same struggle between yellow and red is visible in the genera *Euterpe* and *Pereute*. In *E. tereas* the space is shared, the red keeping to the inner, and the yellow, when present, to the outer side of the precostal nervure. In *P. charops* the space is usually all yellow; in *P. autodice* and *P. leucodrosime* it is all red. In these two genera the other yellow marks are reduced in number or completely abolished; *P. charops*, however, generally has a conspicuous yellow patch between the costal and subcostal nervures which undoubtedly belongs to the series.

In the genus *Pieris*, which is also American, some species, such as *P. locusta* and *P. habra*, show on the under surface of the hindwing a pattern which is evidently only slightly modified from that seen in many

species of *Catasticta;* and in these also the red or orange of the costa is a prominent feature. In other species of *Pieris* a farther alteration has taken place, and the markings have been swept from the basal portion of the wing (as in *P. demophile*), or away altogether (*P. buniæ*). In most, however, if not all of these cases, the precostal streak persists, again taking a yellow rather than red or orange colour; and, in the absence of other yellow or well-defined dark marks on the wing, it comes to resemble very closely the corresponding feature in so many species of *Synchloe* and *Ganoris*.

Summary.—The facts adduced in the course of the foregoing remarks seem so far to allow of little doubt as to the history of the yellow precostal streak. It is evidently a survival of a series of yellow or orange marks which is found, in many genera of both eastern and western Pierinæ, on the underside of the hindwing, partially or wholly occupying the paler areas left between the relics of the original dark ground colour. The greater number of these marks may disappear with a general lightening of the wing, or the whole wing may become so yellow as to render them almost or quite indistinguishable; but the particular yellow streak that occupies the margin of the precostal space is more persistent than any of the others, and may remain, as in our common species of *Ganoris*, after every other characteristic of the ancestral marking has departed. It will be seen later that this account of the precostal streak, though no doubt correct as far as it goes, in all probability needs supplementing.

b. The red basal patch.—In both British species of *Colias*, there occurs at the base of the hindwing, on the under-surface, a pinkish patch, which occupying the apices of the cell and of the median and submedian interspace, and also in most cases a small area at the root of the precostal space, is often prolonged for a short distance along the middle of the cell. This patch, which is almost always present throughout the genus *Colias*, is found in most if not all species of *Meganostoma*, and also very commonly in *Catopsilia, Callidryas, Phœbis, Aphrissa*, and *Metura*. It is present, too, in *Dercas, Gonepteryx, Rhodocera*, and *Amynthia;* in these, however, it does not as a rule extend far from the body itself. Beyond the limits of these closely-allied genera this

special feature does not often occur in a very clearly-marked condition; it is, however, present in *Xanthidia nicippe*, and in several species of *Terias* and *Sphœnogona*, as *T. agave* and *S. mexicana;* it may also be seen occasionally in *Teracolus*, as in *T. antevippe*, *T. eupompe*, and (sometimes) *T. eris*, assuming in this genus a somewhat diffuse appearance. In some species of *Appias*, as *A. hombronii* (occasionally), and *A. lyncida*, as also in *Herpænia eriphia*, there are deep yellow marks near the root of the wing, which are probably homologous with part of the patch now under discussion; and in the genera *Belenois* and *Tatochila* touches of deep yellow often occur at the base of the median space, though not in the cell, which appear to correspond with the marks just referred to in *Appias* and *Herpænia* (see *B. mesentina* and *T. autodice*). These yellow touches in *Belenois* are undoubtedly members of the series spoken of on p. 279, and so far it would seem that the well-marked pink patch at the root of the cell in *Colias*, *Gonepteryx*, etc., is at least in part developed from a portion of that series, of which another member has given rise to the yellow precostal streak. It is certain, however, that other factors besides the series now indicated are chiefly, though probably not entirely, answerable for the composition of the pink basal patch in *Colias;* and it is at least possible, as will presently be seen, that the precostal streak itself owes something to their assistance. These other factors are the red basal areas to which reference has already been made, and which will now be examined in greater detail.

c. The red basal areas. To begin with the underside of *Delias pasithoe*, we find the base of the hind-wings occupied by a bright red patch forming about a quarter of a circle on each wing, the body itself and the immediately surrounding area of the wings being black. The spaces affected by the red patch are six; namely, the precostal, costal, subcostal (or cell), median, submedian, and internal—all those in fact whose apices reach to the base of the wing. In *D. thisbe* there occurs a similar red patch, occupying nearly the same spaces. In this insect, however, there is no red in the precostal space, which is occupied (as above noticed, p. 280) by the ordinary yellow precostal streak; while the red patch, which in this butterfly is visible on the upper as well as the underside

of the wing, includes the apex of the space between the first and second subcostal nervules in addition to those above enumerated. *D. egialea* shows the same condition as *D. pasithoe*; but in *D. crithoe*, otherwise similar, the precostal space is black. In *D. descombesi* and *D. belisama* the red is confined to the costal interspace (*i.e.* the space between the costal and subcostal nervures); while in *D. cœneus* a submarginal set of roughly-defined red spots or dashes continues round to the anal angle the series begun by a red mark in the costal interspace, corresponding with that in the two preceding species. The submarginal series which, so to speak, becomes infected by the red coloration, is undoubtedly that spoken of above as series I (see p. 269). This latter feature of the Pierid pattern, somewhat indefinite in *D. cœneus*, becomes much more distinct in such species as *D. nigrina*, *D. harpalyce*, *D. aganippe*, *D. eucharis*, and *D. argenthona*. The latter of these has another well-marked red spot surrounding the second disco-cellular nervule, which represents a diffused reddish area in *D. duris*, and a more circumscribed patch in the same situation in *D. cœneus*. In *D. hyparete* S is going from the underside of the hindwing; in *D. hierte* it is gone; but in both cases the red spots of I remain in their full development. *D. mysis*, *D. isse*, *D. echo*, and other species exhibit the same feature in a more or less conspicuous manner.

The same red coloration is visible, as we have seen, on the underside of many species of *Prioneris* in the form of a basal patch; and in one species (*P. sita*) it spreads to the submarginal spots of series I, exactly as in *D. eucharis*. In *P. autothisbe* the red is found in the costal and subcostal interspaces; in *P. clemanthe* and *P. vollenhovii* only in the inner division of the precostal space, whence it spreads inwards upon the body.

In the American genera *Euterpe*, *Pereute*, *Leodonta*, and *Catasticta*, the red is usually present; but as in *Prioneris* and the *pasithoe* group of *Delias*, it is mostly confined to the basal portion of the wing.* In *E.*

* An exception to this rule is furnished by *Euterpe tereas* and *E. critias*, in which species the area of light ground colour immediately internal to that region of the wing which corresponds to the submarginal series S, is on both surfaces more or less deeply tinged with the same red colour as that of the basal patches. This feature is due to mimicry, the two species named

tereas, E. critias, C. bithys, and *C. anaitis,* it most commonly occurs in the inner division of the precostal and the internal space; in *Leodonta zenobia* and *L. dysoni,* in the precostal and costal. In *L. tellane,* besides the bright red patches of the precostal and costal spaces, scales of the same colour occur in the apices of the subcostal, submedian, and internal spaces—of all, in fact, except the median. *Pereute leucodrosime* has the precostal and costal red patches; so also has *P. swainsonii*; but in *P. charops* these spaces are occupied by yellow streaks with no accompaniment of red.

Even in the genus *Dismorphia,* profoundly altered as it has been by mimicry, the same marks occur. *D. melia* has a conspicuous red spot in the inner division of the precostal space; while *D. astyocha, D. praxinoe,* and others possess a very clear representative of the same spot, with another one in the median interspace. The colour in these latter species is seldom so bright as in the first-named; it displays, in fact, a tendency to become assimilated to the chestnut tinge of other portions of the wing; the spots are nevertheless quite recognizable, and undoubtedly correspond with those in the former genera. In some species, such as *D. nemesis,* there is no red, but an indication of the yellow precostal streak is plainly visible.

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offering a very close resemblance to the females of *Papilio polymetus* and some of its allies, in bringing about which resemblance the red areas of the hindwing take a considerable share. It is interesting to observe that good as is the general effect of the imitation by these Pierines of the *Papilio* pattern, the imitative process has its limitations, and is seen on a strict examination to fail in more than one particular. Thus, (1) the Pierine is able to produce an excellent representation of the Papilionine reds and yellows, but apparently it never reproduces the metallic blues and greens, of which touches are found in the males of several of the mimicked species; (2) the costal and submedian spaces in the Pierine invariably retain their yellow patches on the underside; these are never yellow in the *Papilio*; (3) the red basal patches on the underside of the Pierine give just the same general effect as similar patches on the *Papilio*; but a close scrutiny will reveal the curious fact that the patches of the Pierine belong always to the wing, and those of the *Papilio,* in almost every instance, to the body. The wide distribution of the red basal patches among the *Pierinæ* forbids us to suppose that they were evolved for the purpose of mimicry in these few species; but it is worth noting that their presence affords material ready to hand for a sufficiently deceptive though not absolutely exact copy of a conspicuous Papilionine feature. See also note on p. 298.

In those species of *Pieris* (such as *P. habra* and *P. locusta*) which present on the underside of the hind-wing a pattern only slightly modified from that of *Leodonta* and *Catasticta*, the red basal marks are clearly to be distinguished. A bright red patch characterises the inner division of the precostal space, and in most specimens is also prolonged into the outer division, while the apices of the median and internal spaces are likewise provided with conspicuous red touches. Comparing the underside of *P. locusta* with that of any of the American mimetic forms of *Mylothris*, we cannot well resist the conclusion that the central horizontal red or chestnut band in the latter species represents the touches of red in the median and internal spaces of *P. locusta*. The relation is best traced in the case of *M. lypera*, in which insect the part played by the yellow streak of the costal interspace in the production of the mimetic pattern is also clearly to be seen; but other species, such as *M. lorena* and *M. pyrrha*, whose mimicry of Heliconine forms is further advanced than that of *M. lypera*, still show the origin of the central red band almost equally well. In *Hesperocharis hirlanda* a somewhat similar effect is produced by slightly different means. The basal red is here confined to the precostal and internal spaces, not being found (as in *Pieris*) in the median. The horizontal red band is therefore not central but costal, its innermost extremity being constituted not (as in *Mylothris*) by the red patch of the internal space, but by that of the inner division of the precostal. The whole of the precostal red, which is absent in the three species of *Mylothris* just referred to, is prominent in *H. hirlanda*. Although these differences involve a change in the relative position of the horizontal bands of red and pale yellow in the latter species, yet the general resemblance of the underside to that of *M. pyrrha* ♂ is considerable, and is probably quite enough to tell perceptibly in the insect's favour. Other species of *Hesperocharis*, which are unaffected by mimicry, show the basal marks in the same position, but, as a rule, not very definitely, except at or near the root of the precostal space. Here there generally occurs an orange spot which partly represents the red precostal patch in *H. hirlanda* (see *H. nereis*, *H. marchalii*, and *H. anguitia*), but which in some species (as

H. erota) can be distinctly seen to belong to the apex of the median interspace as well as to the root of the precostal.* A similiar orange spot is visible in several species of *Pieris*, such as *P. buniæ* and *P. thaloe*; and of *Leptophobia*, as *L. elodia* and *L. eleusis*. In the last-named insect again it can generally be made out that the orange spot does not belong entirely to the root of the precostal space, but is furnished with a constituent from the apex of the median interspace as well. This double character of the spot is much more evident in *L. tovaria*; and on referring once more to almost any species of *Colias*, the conviction forces itself strongly upon us that in these basal marks in *Leptophobia*, *Hesperocharis*, and *Pieris*, and so in *Euterpe*, *Leodonta*, *Catasticta*, and consequently even in *Delias* and *Prioneris*, we see represented the chief material out of which the pink basal patch in *Colias*, *Gonepteryx*, *Catopsilia*, and their allies is constructed. It is probable that, as above suggested, another element may enter into the composition of the basal patch in these genera, namely one or more members of the series of yellow streaks; a conclusion which seems to be somewhat favoured by the condition in *Belenois*, *Herpænia*, and *Appias*; but the two series are distinct enough from one another in such genera as *Catasticta* and *Leodonta*; and an unnamed species of *Hesperocharis* in the British Museum shows, still more plainly than those above mentioned, the co-existence of a relic of the basal red in the situation of the pink patch in *Colias*, with a series of yellow streaks in the interspaces like those of *Catasticta* and *Belenois*.

Summary.—With regard to the whole assemblage of red and yellow marks on the underside of the hind-wing, the following appear to be the most probable conclusions:—

The yellow precostal streak so commonly seen in butterflies of this group, including our common British species of *Ganoris*, as also the pinkish patch at the apex

* In order to avoid a possible ambiguity, I may here mention that I regard the "apices" of the interspaces as pointing towards the "base" of the wing. When a precostal nervule is present, I speak of an "outer" and "inner" division of the precostal space, the nervule forming the line of demarcation. By the "root" of the precostal space, I mean the part immediately adjoining the body.

of the cell, of which our native species of *Colias* and *Gonepteryx* present good instances, are relics of a more elaborate system of marking seen in a high condition of development in various exotic genera. This system consists essentially of a series of red and yellow markings occupying more or less completely the pale spaces included between the radially disposed dark lines that coincide with the nervures on the one hand, and the concentrically arranged dark spots or bars of the marginal and submarginal series on the other. That this system of markings is a very primitive one is rendered probable by the fact (1) that it is represented by vestiges in so many genera of both hemispheres; and (2) that it occurs in a well-developed condition in genera so widely separated in a geographical sense as the South American *Leodonta* and *Catasticta*, and the Australian and Indian *Delias* and *Prioneris*. As a general rule, the spaces at the base of the wing tend to be occupied with red, and those on the disc and at the periphery with yellow; but in some cases, as has been seen, the red may encroach upon the submarginal yellow (as in *Delias cœneus*, *D. eucharis*, *D. argenthona*, etc.), or may be prolonged from the base in various directions across the wing (*Hesperocharis hirlanda*, *M. lypera*, *M. pyrrha*, and other American species of *Mylothris*). In the first-named genera, which exhibit the system in its full state of development, the distinction between the red and yellow markings is a perfectly easy one; but in such genera as *Pieris*, *Leptophobia*, *Hesperocharis*, *Belenois*, *Ganoris*, *Synchloe*, and *Colias*, whose markings are no doubt ultimately derived from the *Catasticta* and *Delias* pattern, it is not always easy to say to which part of the original system the relics that are present belong. On an inspection of all the forms, it would, however, seem to be the case that those members of the yellow part of the system most often persist which are capable of being reinforced, as it were, by a neighbouring red patch towards the base of the wing. For instance, the most persistent marking of all is, as we have seen, the yellow precostal streak. This is in most species of *Leodonta* and *Catasticta* closely bordered on by a bright red spot in the inner division of the precostal space; and on tracing the condition of that space from these more ancestral genera downwards, through *Pieris*, *Leptophobia*, and

Hesperocharis, we find it become tolerably evident that the dark yellow vestige which at last alone remains is the result of a kind of convergence both in colour and position of the yellow and red markings that at first lie simply side by side and are clearly distinguishable the one from the other.* A further instance of possible convergence is supplied by the basal pinkish patch, found in the group of genera headed by *Colias*, which we have seen reason to identify with original markings of both the red and yellow kinds.† In other cases, the persistence of various members of the present system is determined by the exigencies of a mimetic pattern, as in the species of *Mylothris* and *Hesperocharis* above referred to (p. 286).

III. Phylogenetic Conclusions.

1. *The evidence of the Wing-markings.*

We are now in a position to consider as a whole the various sets of facts that have been above recounted, and to endeavour to construct, from the evidence at hand, a theory of the phylogenetic history of the entire group. This, of course, is only attempted under the

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* This, it is true, applies only or mainly to the New World forms ; the similar basal red patch that partly occupies the precostal space in certain species of *Delias* and *Prioneris* not seeming to have left any traces in those Old World genera (*Belenois* and *Teracolus*), which appear to stand in much the same relation to *Delias* and *Prioneris* as *Pieris* and *Hesperocharis* do to *Leodonta* and *Catasticta*. The deep orange, however, of the precostal streak in some Old World species of *Mylothris* (as *M. chloris* and *M. agathina*), and in some species of *Belenois* (as *B. helcida*) which resemble them, may perhaps be derived wholly or in part from the precostal red ; but if so, it does not bear in itself a plain record of its origin as does the like feature in the corresponding genera from America.

† Again, in *Pieris pylotis* the only marking to be seen on the under surface of the hindwing (besides the basal spot) is a short and narrow orange streak near the apex of the median interspace—an interspace that in more primitive forms, such as *P. locusta*, *Mylothris lypera*, and others, is provided with an apical red patch. It is also worthy of notice that in many species of *Belenois* the spots of series I are apt to retain or assume an unusually deep yellow or orange colouring like that of the precostal streak—this series being in some species of *Delias*, and at least one of *Prioneris*, a sharer in the bright red of the basal patches (see p. 284).

limitations above referred to, and is not to be taken as more than a connected statement of the probable import of the facts derivable from one particular source—those facts, namely, which relate to the colours and markings. I need hardly say that I recognise to the full that any phylogenetic conclusions founded on these data must of necessity be open to checking and correction in the light of information arrived at in other ways.

The evidence that has now been examined seems to indicate that the wings in the earliest form of Pierine were uniformly overspread with a dark neutral tint.* The first variation from this condition appears to have occurred by the paling of certain areas in the principal interspaces between the nervures; a modification that may be seen in probably its simplest extant form in the remarkable American Pierine *Eucheira socialis* (Fig. 1). Here each interspace, including the discoidal cell in both wings, possesses a more or less definite pale patch, those of successive interspaces being so arranged as to form a somewhat indistinct and interrupted band crossing the disc of both wings from the costa to the inner margin. Besides this central series of pale patches, there is also a submarginal row of much smaller and fainter spots of the same greyish-white hue. The whole pattern is repeated with very little change on the under surface, but on the hindwing with even less distinctness than above. The underside of the hindwing in this insect, indeed, probably exhibits the very oldest kind of Pierine colouring to be seen in any existing species.†

The primitive system of marking manifested by *Eucheira socialis* persists with little alteration on the upper surface of many species of *Catasticta*, as, for

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* This accords generally with the opinion expressed by Mr. Wallace: "There are, in fact, many indications of a regular succession of tints in which colour development has occurred in the various groups of butterflies from an original grayish or brownish neutral tint."—"Darwinism," 2nd edition, 1889, p. 274.

† While entirely agreeing with Staudinger and Schatz that the remarkable forms *Styx infernalis* and *Pseudopontia paradoxa* are probably of great antiquity, I cannot but regard the special Pierine affinities claimed for them by these authors (and especially for the latter) as more than doubtful. See Staudinger, Schatz, and Röber, "Exotische Schmetterlinge," 1892, *sub voc.*

instance, *C. bithys* (Fig. 2), *C. toca*, and *C. colla*. In other species of the same genus, the next steps are shown by the enlargement of the pale spots (as in *C. anaitis* ♂), their assumption of a purer white colour (as in *C. anaitis* ♀), and the confluence of those of the inner row, as in *C. trœzene* and *C. ctemene* ♂. In the latter insect the enlargement and confluence of the white patches has proceeded so far that the white must now be considered the ground colour, the original dark neutral tint being confined to the base and apices of the forewings, a narrow and interrupted marginal band on the hindwings, and the course of the nervures with their branches (Fig. 3). In *C. corcyra*, the same process is continued almost to its furthest limit, the new ground colour has supplanted the old in every place except the apex and a narrow slip along the costa of the forewing. *C. corcyra* is thus practically a "white" butterfly; and so within the single genus *Catasticta* a complete transition is to be found, from a dark almost black ground colour, with small and indistinct pale greyish patches, to a ground colour of dead white, with hardly more than a trace remaining of the original dark surface tint. This passage from *C. bithys* to *C. corcyra* is really an epitome of the whole range of variation in pattern throughout the entire group of *Pierinæ*.

In such species of *Catasticta* as *C. semiramis*, where the pale patches are tolerably distinct, and have not yet coalesced, the dark marginal and submarginal series of spots, so characteristic of the Pierines as a whole, are visible at an early stage of their emergence. As has been shown above, on p. 267, the marginal series (called M) is formed by the remains of the dark ground colour between the outer series of primitive pale patches and the outer border of the wing; while the submarginal series S comes into view between the outer and inner series of pale patches. Besides these, a relic of the dark ground colour is seen to remain about the disco-cellular nervules in the forewing, which forms the first beginning of a definite discoidal spot; and another row of minute pale patches, each occupying the centre of an interspace on the extreme outer margin of the wing, begins to split up the marginal series in the manner already spoken of. The definite character of series M is assumed sooner on the forewing than on the

hindwing, and in the latter situation the discoidal spot has at this stage scarcely become recognizable; in some species, however, a patch of pale-coloured scales covers the lower disco-cellular nervule of the hindwing in the midst of a wide and not sharply-defined area of dark ground colour.

So far little or no essential difference has been noted from the primitive pattern of *Eucheira socialis*; the variations produced having simply resulted from a greater or less extension of the intrusive pale tint along the lines originally marked out. But, on turning to the underside of any species of *Catasticta*, we find what at first sight appears to be a very considerable divergence. A careful examination, however, soon makes it plain that the pattern of the lower surface is throughout the genus essentially the same as that of the upper surface, though one or two new features are superadded. Confining our attention in the first place to the forewing, for instance in *C. nimbice*, we find the submarginal series S and the discoidal spot shown at least as clearly as on the upper side; while from the greater prominence of the pale spots at the extreme margin, M is brought still more plainly into view below than it is above. On the hindwing, the central pale band may be easily traced across the disc of the wing, leaving on the one side of it a basal, and on the other a broad marginal dark area. Traversing the latter can be seen a row of elongated, more or less wedge-shaped, yellow streaks, which represent the more easily recognized series I of the forewing; while a distinct row of yellow spots on the extreme margin continues the similar series from above. Though S and M are not yet sharply marked off from one another, the portions of dark ground colour to which they respectively belong are already separately recognizable. The undersides of *C. nimbice*, *C. colla*, *C. toca*, and *C. corcyra* will be found to make a very good transitional series, showing the gradual emergence of S and M and the subsequent reduction of each to a mere festooned line.* The superadded features above alluded

* An unnamed species of *Catasticta* in the British Museum presents a condition of the underside of the hindwing more exactly intermediate between *C. corcyra* and the usual type than any of the species mentioned. An individual of the same species is in

to are (1) the streaks and touches of yellow that begin to occupy much of the area of the original pale patches, including, as has been seen, the spots of I on the hindwing; and (2) the bright red patches visible in the basal region of the same wing close to the body. These have been already discussed at some length (see pp. 281, 285), and their importance has been shown in reference to the markings of more recent groups. In this place it is only necessary to note once more that their ancestral character seems to be proved not merely by their existence in a fully developed condition in genera so widely separated geographically as the Western *Catasticta* and *Leodonta* and the Eastern *Prioneris* and *Delias*, but also by the fact that there is scarcely a genus throughout the whole sub-family, whether in the Old or New World, that does not show some relic of their former presence. With regard to their origin, no clue appears now to exist. It seems impossible to trace them further back than to the Eastern and Western genera named; and the probably still more primitive form, *Eucheira socialis*, to which we should naturally turn for an indication of their development, affords us in this particular no information whatever.

In the genus *Leodonta* we find some modification in the shape of the wings, and only three instead of four branches to the subcostal nervure of the primaries. But the wing pattern remains much the same as in those species of *Catasticta* where the white central band has grown into a well-defined area and the two series S and M have not yet become clearly distinguishable. The yellow streaks and red basal marks are still prominent on the hindwing beneath, and the separation between S and M is, in this genus also, more evident on the underside.

In *Pereute* and *Euterpe*, which are undoubtedly very close allies of the genera just referred to, the development of the pattern has taken a somewhat different direction. The primitive dark ground colour is in the males of several species of *Pereute*, as *P. charops*, *P. autodyca*, and

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the Hewitson collection labelled as *C. notha*. This is undoubtedly erroneous, as the underside of the true *C. notha* is almost exactly like that of *C. corcyra*.

P. swainsonii, relieved by dustings of pale pinkish or bluish grey, which do not seem to bear any particular relation to the lighter patches in *Catasticta* or *Eucheira*. These greyish areas are often, especially in the females (including those of the species named), brightened up into bars or broader expanses of vivid red (*P. leucodrosime*) or blue (*P. telthusa*), and the aspect thus produced is very unlike that of nearly all the members of the allied genera. But as has been shown above, at pp. 281 and 285, an indication of affinity in coloration with those genera is preserved in the red and yellow patches of the underside of the hindwing; and, what is very remarkable indeed, there are two species of *Catasticta*, namely *C. teutamis* and *C. ctemene*, the males of which are of the usual *Catasticta* type, while the females present, together with the ordinary *Catasticta* neuration and structure, the aspect characteristic of *P. charops* ♀ and other highly coloured members of the genus *Pereute*. In the case of these two *Catastictas* there can, I think, be no doubt that it is the male rather than the female that represents the ancestral colouring of the group, and we are thus led to the conclusion that some common cause has brought about the divergence in the same direction of these female *Catastictas* and both male and female *Pereutes* from the ordinary character of their nearest relatives. This cause I believe to be mimicry, the models for which in the present instance are to be found in certain species of *Heliconius*, particularly *H. melpomene*, *H. phyllis*, and their allies.* The resemblance is not perfect,† but in all probability is quite sufficient to be of much service to the Pierine mimics; and we find exemplified here, as in many other cases, the much greater readiness with which the female assumes the protective coloration. As we

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* I also think it exceedingly likely that *Papilio euterpinus*, Godm. & Salv. (Ecuador), forms one of this mimetic group. It is, however, remarkable that its range seems not to coincide with that of the Pierine, namely *P. charops* ♀, which probably resembles it most closely in size as well as colour.

† The red colour of the species of *Heliconius* here mentioned (to which may be added *H. vulcanus* and *H. hydara*), as they occur in collections, is by no means so vivid as that of their supposed imitators. But Mr. A. G. Butler and Mr. F. A. Heron both inform me that the red in *Heliconii* has a special tendency to lose its brightness, even in specimens carefully preserved in the dark.

have seen, the male *Catastictas* are not affected at all; while in most species of *Pereute* the males have not advanced nearly so far along the mimetic path as have the females. Another point worthy of observation, which is paralleled elsewhere, is the fact that the males show a much closer approach to the complete mimetic pattern on the lower than on the upper surface.*

A similar explanation will apply to the even more remarkable divergence shown by the genus *Euterpe*, though here the phenomena are so curious and complex as to require a more detailed treatment. This genus (as restricted by Butler, Cist. Entom. i., pp. 34, 42) does not contain a single form that reproduces in general aspect the typical Pierine features; every species indeed is the subject of a mimetic change, and such marks of their origin and relationships as they retain, are used up in a more or less modified condition to help in the production of the deceptive pattern. Thus we have seen how in *Euterpe critias*, *E. tereas*, *E. rosacea*, and allied species, the area representing the white central band on the hind-wing, now tinged with rosy pink, has become an important ingredient in the general imitation of *Papilio zacynthus* ♀; the red basal patches on the under surface also taking their part in the picture. There is, moreover, little doubt that the white spot on the forewings is identical in origin with the usual white central bar, while for the marginal yellow spots a counterpart is easily found in *Catasticta nimbice* and many of its allies. In *Euterpe bellona* we find the patch on the forewings bright yellow instead of white, while the rosy patch is intensified in colour and split up into three or four brilliant streaks radiating from the base towards the margin of the wing. The general effect is not very dissimilar from that of *E. critias*, and the identity of the markings is beyond question; nevertheless the changes, slight as they are, are highly significant, for they import nothing less than the substitution of a member of the Heliconine for one of the Papilionine group as a model for imitation. *Euterpe bellona* undoubtedly mimics the Heliconine group of which *H. thelxiope* and *H. burneyi* are conspicuous members; and it would be difficult to find a better instance to show how slight a

* See Weismann, "Studies," vol. i., pp. 7, 8 (English Edition).

modification of an existing pattern may suffice to produce an effective copy of an entirely different insect. Facts of this kind seem to go a long way towards answering such objections to the theory of mimicry as those alluded to by Mr. Beddard in his "Animal Coloration," 1892, pp. 214, 215.

It is very remarkable that red basal patches, like those of the mimicking Pierines, occur on the underside of the hindwing in most, if not all, of the Heliconii and Papilioninæ mimicked by members of the genera *Pereute* and *Euterpe*; and in some, *e.g.*, *H. melpomene*, there is even a well-defined yellow precostal streak. Now although there is no difficulty in ascribing most of the features in the coloration of these Pierine genera to the operation of mimicry, it would seem, for the reasons given above (p. 285, note), that the origin of these particular marks, which are so wide-spread and so persistent throughout the whole Pierine subfamily, must be excepted. Nor, in the absence of any evidence of a direct causal relation, does it seem to my mind more satisfactory to consider the occurrence of these patches in the three diverse groups, Papilionines, Heliconines, and Pierines, as the effect of similar external conditions. If we assert them to be purely "accidental," we are met by the fact that although they are found in some species of both *Papilio* and *Heliconius* that are apparently not the subject of mimicry, yet they are most distinct and most prevalent in those species that are copied by Pierine imitators; and the same considerations (amongst others) seem to show that the supposition that they are simply due to inheritance from a common ancestor of all the groups must be inadequate. Before the phenomenon is dismissed as inexplicable, it may be worth while to consider the following suggestion.

According to the well-known principle laid down by Fritz Müller and expanded by Meldola, by which these authors have been enabled to account for cases of parallel resemblance between the species of protected genera, and also of the grouping of allied inedible species into distinct sets, each with its own scheme of coloration,* it

* F. Müller in "Kosmos," 1879, p. 100; Meldola in "Proc. Ent. Soc. Lond.," 1879, p. xx., and "Ann. and Mag. Nat. Hist.," Dec., 1882. See also Wallace, "Darwinism," 2nd ed., 1889, pp. 249–257, and Poulton, "Colours of Animals," 1890, pp. 192–195.

is advantageous for any two or more protected species to join their forces, in order to share the toll levied upon them by inexperienced enemies. In such cases it no doubt often happens that one species serves as the standard to which the others conform, whether by way of convergence or of arrested divergence; but there seems no reason why, especially if there is no conspicuous inequality of numbers, there should not be a kind of "give and take" arrangement between mimicker and mimicked, the latter advancing some way to meet the former for their mutual benefit. In other words, when two species, A and B, form an association of this kind, it need not be supposed that the form of A remains fixed, while B assimilates itself to it, or *vice versa;* but the association may really be formed by both A and B converging towards a point between them, or, in short, mimicking each other. The acceleration of the process which in many cases would result, must of itself be an advantage. Now if the grouping of kindred inedible forms in associations of this kind is beneficial, it would seem that the benefit might extend to members of families far removed from one another, like the three now under discussion, as well as of the same family or genus;* the only requisites being (1) that all should be more or less inedible, and (2) that all should have patterns capable of assimilation to one another. Nor does there seem to be any reason why a *mutual* convergence of the kind indicated should not take place under these conditions also. With respect to (1), it has, I think, nearly always been assumed that the *Pierinæ* which resemble the members of other families are edible; and this is no doubt the case with the numerous members of the genus *Dismorphia* † (*Leptalis* of Dalman), which were among the first to attract notice to the subject of Mimicry in general. But no direct proof seems to exist that the species of *Euterpe* and *Pereute* now under discussion are edible; and indeed Mr. Wallace considers (Trans. Ent. Soc. Lond., 3rd series, iv., pp. 309, 310; Darwinism, 2nd ed., 1889,

* Such an association is already well known to occur between *Heliconidæ* and *Danaidæ*.

† This, however, has been questioned by Mr. Beddard, who cites some observations of Scudder as tending to show the contrary. See "Animal Coloration," 1892, p. 215.

p. 244) that the genus *Delias* (*Thyca* of Wallengren), which is probably nearly related to *Euterpe* and *Pereute*, possesses a disagreeable flavour, or some other special means of protection. If this is shared by its American relatives, the first of the above requirements would be satisfied, while the second (2) has been shown to be met, in the special instance of the red basal patches, by the occasional presence of somewhat similar spots or patches (whose origin is not now under discussion) in other species of both the Papilionine and Heliconine groups, which afford quite sufficient material for the assimilative process to work upon. Until, therefore, direct proof is forthcoming of the edible qualities of the Pierines in question, it will not be unreasonable to suppose that they have joined an "inedible association," and to attribute this curious agreement in a detail of pattern between members of such diverse groups to the operation of what may perhaps be called "reciprocal mimicry."* The Pierines have no doubt moved furthest from their original form, having in most respects clothed themselves in Papilionine and Heliconine colours, but the latter have themselves advanced some way to meet the Pierines, in adopting from them a more distinct and characteristic employment of the red basal patches.†

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* This, it will be seen, is distinct from "convergence" in the usual sense, inasmuch as that term has hitherto been employed (as by Poulton, "Colours of Animals," 1890, p. 195) to signify the assimilation of one form to another, rather than the mutual approach by two forms to a mean between them.

† Fritz Müller notes ("Kosmos," 1879, p. 100, and translation by Meldola, Proc. Ent. Soc. Lond., 1879, p. xxiv.) that "in the province of Santa Catharina, *Euterpe tereas* is common in the forest-paths almost throughout the entire year, while its model, *Papilio nephalion*, is, on the other hand, a rare butterfly." This is so far in favour of the supposition that the resemblance is not due to mimicry by the Pierine, at least in the strict sense.

There is one more piece of evidence that seems to favour the conclusion arrived at above. So far as I am aware no explanation has yet been offered of the fact that it is the females and not the males of *Papilio polymetus*, *P. zacynthus*, etc., that are resembled by *Euterpe tereas* and *E. critias* ; whereas the males, which display brighter colours, afford at least as good if not better models for imitation. I would suggest that this is really due to "reciprocal mimicry." The protection gained by the resemblance between the Pierines and Papilios is not all on the side of the Pierines, but mutual ; and the female Papilios have, as is usual, felt the need of it more urgently than the males. For this reason the female

Euterpe theano and *E. eurytele* present us with another kind of departure from the ordinary Pierine condition, the latter being an excellent copy of *Lycorea atergatis* and *Ceratinia* (*Ithomia*) *dionæa;* while *E. theano* exhibits the form of *E. eurytele* with a coloration much like that of *Pereute charops* ♂.

We find then that, thus far back in the growth of the Pierine stock, a large section has been diverted under the influence of mimicry from the regular course of development of the Pierine pattern; and in order to continue the history of the latter, we must retrace our steps and take up the thread where we left it before beginning to discuss the mimetic forms of *Pereute* and *Euterpe*.

Although it does not appear that the Old World can show any truly Pierine form so ancient as *Eucheira socialis*, there does exist a genus which seems to represent in the East nearly the same stage of development as *Catasticta*, *Leodonta*, *Pereute*, and *Euterpe* in the West. This is the genus *Delias*, the close relationship of which with the western forms mentioned has been indicated by Doubleday and Westwood (Genera of Diurnal Lepidoptera, vol. i., p. 33), and more distinctly suggested by Wallace (Trans. Ent. Soc. Lond., 3rd series, iv., p. 344).* The pattern of *Delias belladonna* is essentially similar to that of the early *Catastictas*, consisting as it does of a dark ground-colour relieved by paler touches in the interspaces, between which touches the ground-colour is already beginning to show a rudimentary division into a marginal and submarginal chain with a vaguely indicated discoidal patch in each wing. On the underside we have the same pattern in a slightly more distinct form; while, as in *Catasticta*, the pale areas of the hindwing and the apical region of the forewing are furnished with yellow streaks. The red basal patches, so characteristic of

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Papilios have been led to meet the Pierines by discarding, or at any rate by not adopting, the bright metallic blues and greens that ornament the other sex. This was no doubt a shorter and easier way to the formation of an "inedible association," than would have been the acquisition by the Pierines of colours more nearly resembling those of the male Papilios.

* *Delias* agrees closely in neuration with *Pereute* and *Leodonta*. See Butler, Cist. Entom., i., p. 40. Staudinger and Schatz, "Exot. Schmetterl.," 1892, Theil. ii., p. 63.

Catasticta and its allies, are not represented in *D. belladonna*, but in all the members of the *pasithoe* group they are not only present, but have become a very conspicuous feature in the coloration. It is not difficult to bring the other markings of *D. pasithoe*, *D. thisbe* and their allies into relation with those of *D. belladonna*, though the dark series S and M are as a rule less clearly indicated. The *pasithoe* and *belladonna* groups of *Delias* may thus be considered as on the whole the most ancient.* In the well-known *D. eucharis* we have the series S and M complete; the female, as is usual, showing less departure than the male from the more generalised form. As in *Catasticta*, no sooner have the dark series emerged into distinct existence than they begin to disappear; they are much less recognizable in *D. hyparete* and *D. agostina* than in *D. eucharis*, and in *D. hierte* they reach the vanishing point. *D. eucharis* and its immediate allies follow the early condition of *Delias* in having the interspaces on the underside of the hindwing more or less filled in with yellow, but they depart from it in having lost the red basal patches, and in possessing a conspicuous submarginal band of red spots (series I) between the dark series S and M; these are best seen in *D. eucharis* itself. An early stage of this red series is probably present in *D. cœneus* and the closely allied *D. philotis*, which seem to be linked with the still more primitive butterflies of the *pasithoe* group through such forms as *D. belisama* and *D. descombesi* (see p. 284). Regarding then *D. cœneus* as a new starting-point, we may trace from it in one direction the Indian group headed by *D. eucharis*, and in another the Australian forms *D. aganippe*, *D. harpalyce*, and *D. nigrina*. It is to be observed that both *D. eucharis* and *D. aganippe*, though probably more recent than *D. cœneus* so far as regards the underside of the hindwing, nevertheless retain in other respects more of the primitive pattern; from which we may probably conclude that some form now lost, rather than *D. cœneus* itself, supplies the true link with the *belisama* and *pasithoe* groups, while *D. cœneus* and *D. philotis* survive to show how "series I" acquired in

* I follow, in nearly every particular, Mr. Wallace's division of this genus into groups. See Trans. Ent. Soc. Lond., 3rd series, iv., p. 344, etc.

the *eucharis* and *aganippe* forms its conspicuous character. I have little doubt that the curious form *D. aganippe* is one of the oldest existing species of *Delias* in the Australian region, inferring this from its retention of the primitive series S and M with the discoidal patch in the forewing in fairly distinct form, from the presence of yellow streaks in the interspaces of the under surface, and from the occurrence of a basal red spot in the precostal space of the underside of the hindwing. Many of these points assimilate it to the *pasithoe* group, and even more closely to *D. belladonna*.* *D. harpalyce* and *D. nigrina* seem to follow naturally on from *D. aganippe*, though in respect of the *costal* red they are perhaps a little nearer the still more primitive *D. belisama*. Another Australian offshoot of the *D. cœneus* stock is probably represented by *D. argenthona*, *D. mysis*, *D. isse*, and *D. dorimene*. The Indo-Malayan and Australian *nysa* group is probably derived from the *pasithoe* and *belladonna* groups through *D. orphne* and *D. momea*. It would be most interesting to attempt to trace in detail the phylogenetic history of the whole of this extensive genus, but it must here suffice to have indicated what appear to be the principal lines of derivation. Two points of analogy with the kindred neotropical genera may be noted before we pass on. The first is that although the invasion of a paler tint does in *Delias* tend to split the original ground-colour into marginal and submarginal series quite similar to those of *Catasticta*, and though these series in various stages of development and suppression, as also in *Catasticta*, meet us here and there throughout the entire genus, yet in many cases the series never emerge in any recognizable form, and there seems in several species a tendency for the white invasion to begin near the bases of the wings, and simply sweep the dark ground-colour away towards the margins. Even in these cases, however (as in *D. belisama* and *D. descombesi*), the females, on the underside, will usually show some indication of the primitive series. The second point to be noted is the way in which the resources of Pierine coloration are taxed to give the insects of this genus a brilliant appearance. As in the case of some of their neotropical congeners, this is effected not so much

* See Wallace in Trans. Ent. Soc. Lond., 3rd series, iv., p. 349.

by the importation of any new feature as by the brightening up and extension of features already present, and indeed often common to the whole subfamily. The reason for this ornamentation is doubtless the same in both cases—namely, to call attention to inedible qualities. The Eastern genus, however, seems to have itself become a model for mimicry (Wallace in Trans. Ent. Soc. Lond., 3rd series, iv., pp. 309, 344), while the Western genera have modified their ancestral form in order to join an alien company of inedible insects.

The genus *Prioneris*, though differing slightly from *Delias* in neuration and other structural characters, is probably nearly akin to it, and represents, so far as the colouring is concerned, a similar degree of antiquity in the Pierine stock. The close resemblance of pattern between different species of *Delias* and *Prioneris*, to which reference has already been made (pp. 258, 284, etc.), is no doubt a true case of mimicry, but represents probably the result rather of arrested divergence than of the acquisition by *Prioneris* of new imitative features.

The two groups that have just been discussed, namely, those formed by *Delias* and *Prioneris* in the Old World, and by *Catasticta*, *Leodonta*, *Euterpe*, and *Pereute* in the New, thus constitute together a second grade, as it were, in Pierine development. The only earlier species yet mentioned is *Eucheira socialis*, but there exist certain other forms which appear to be but little inferior to that insect in antiquity; and to these, with *Eucheira*, the name of "Pierines of the first grade" may be applied. One of the forms now referred to is *Metaporia agathon*. This remarkable insect is probably the representative of an ancient group of Pierines, among which were to be found the common ancestors of the two second-grade assemblages already mentioned, and which, no doubt, supplied the link at present wanting between *Eucheira* and *Catasticta*. The relation of *Metaporia* with the Eastern assemblage is more direct than with the Western, for although it offers points of structural difference from *Delias*, it shows, nevertheless, a condition of the primitive Pierine pattern which is in all essentials identical with that of the earlier kinds of that genus. The correspondence of its markings on the upper surface with those of *Delias belladonna* and *D. eucharis* is at once evident, and, like *D. belladonna*, it has a patch of bright

yellow in the precostal space on the under surface of the lower wings. This, however, is usually confined to the inner division of the space.* Mr. Wallace† considers that *Metaporia agathon* forms with *Pontia nabellica* the fragments of an extensive natural group. He also points out the readiness with which the pattern of *M. agathon* can be traced through *P. nabellica, P. soracta,* and *P. hippia,* to its final disappearance in *P. cratægi.* In this range of species, to which may be added *P. oberthüri, P. leucodice, P. belucha,* and others, we recognise the now familiar phenomena of the emergence, establishment, and evanescence of a marginal and submarginal series of spots, together with a discoidal patch, formed out of relics of an original dark ground-colour. Another primitive Pierine feature, namely the persistence of dark ground-colour along the course of the nervures and nervules, is found throughout the group; and in *P. cratægi* survives the disappearance of almost every other indication of the original coloration.

The line thus marked out ends with *P. cratægi*; but in another direction there is little difficulty in linking *Pontia* with *Eucheira,* and so demonstrating the intimate connection with one another of the three last-named genera. Thus *Pontia* recalls *Eucheira* by the outline of its wings, especially the concave costal margin,‡ and in pattern *P. nabellica* shows no very great departure from the same genus. But a more striking sign of affinity exists in the common larval habitation, which, though merely rudimentary in *P. cratægi,* and belonging only to the early larval stages, is no doubt a degenerate or undeveloped form of the elaborate silken nest constructed by *E. socialis.* Webs of a structure apparently comparable with the latter are made by *Neophasia terlootii* and an allied species mentioned (though not described) by Behr.§ The affinity of the two latter insects with the genus *Pontia* appears certain; and though Behr is perhaps wrong in making them con-

* One specimen of *M. agathon* in Coll. Brit. Mus. has a few orange scales in the *outer* division of the precostal space as well.

† Trans. Ent. Soc. Lond., 3rd series, iv., p. 313.

‡ Noticed by Staudinger and Schatz, who compare it to that of *Parnassius*, Exot. Schmetterl., Th. ii., p. 62.

§ Trans. Amer. Ent. Soc., 1869, p. 303; Proc. Calif. Acad. Sci., second series, vol. ii., 1890, p. 91.

generic with *E. socialis* (which he does not seem to have seen.),* his description, nevertheless, renders it extremely probable that they are more closely related to that species than any other known butterfly. The Pierines of the first grade may accordingly be said to consist of *Eucheira*, with Behr's two "*Neophasias*," *Pontia* and *Metaporia*. The prevalent larval habit of spinning is no doubt an indication of the high antiquity of the group, and suggests, as do other features, a relationship with the Parnassids. This suggestion is further borne out by the aspect of *Mesapia peloria*, which is no doubt an offshoot of the genus *Pontia*. But such relationship is certainly of no close or direct kind, and is probably only referable to an extremely remote ancestor of the two subfamilies.†

Leaving the genus *Pontia* for a time, we may make a fresh start with *Metaporia agathon*, from which point it is not difficult to trace another principal stem, with numerous and important ramifications. The females of several species of Mr. Moore's genus *Huphina*, for instance *H. phryne* ♀, show what is to all intents and purposes the same pattern as *M. agathon* (Figs. 7, 8); and the males differ only or chiefly by the more ready admission of the white invasion, at the expense of the remains of dark ground-colour. The pattern of such a form as *H. nama* ♀, seems at first sight to belong to a different category, but a very good transition from that of *M. agathon* is afforded by *H. eperia* ♀, which shows how the arrangement of white patches in *H. nama* ♀ has grown out of the discal and cellular white, while the more marginal series I sinks gradually into the background, and with its disappearance the two dark series S and M lose of course their distinctive character. In one ancestral point, namely the filling up to a greater or less extent of the interspaces of the hindwing underside with yellow, *Huphina* shows a closer resemblance to *Delias* and *Prioneris* than to *M. agathon*, in which insect this feature is only slightly indicated. In many species

* *N. menapia*, included by Behr in the same genus, differs from *Eucheira* is neuration and other points.

† *Davidina armandi* has been spoken of as a transitional form. But, as remarked by Staudinger and Schatz (*op. cit.*, Th. ii., p. 57), it is shown by Oberthür's figure (Etudes, iv., pl. ii, fig. 1) to be without any of the points characteristic of the Papilionidæ.

of *Huphina* the yellow is very vivid, in some it is warmed into a rich orange, and it not infrequently, as in *H. naomi*, *H. lea*, and *H. judith*, appears on the upper surface as well.

From the pattern of *Huphina* to that of *Catophaga* the passage is easy through such species as *H. cassida*, *H. nabis*, *C. paulina* (Fig. 9), and *C. ega*. In the latter genus, as in the former, the dark ground-colour is retained in much larger measure by the females than by the males; the latter indeed (as in most specimens of *C. galena* ♂) have often lost it altogether. Other marks of specialization shown by the male *Catophagas* are the sharply-pointed shape of the wings, and, above all, the presence of a tuft of long hairs springing from the base of each of the anal valves. All these characters belong equally to the next genus *Appias* (which indeed is not easily to be distinguished from *Catophaga*), though here the specialization of the males has in many forms been carried to a much greater extent, and is occasionally in some respects shared by the females, as in *A. nero*. In this insect the female shows the remains of the usual dark marginal and submarginal series standing out upon a ground colour of rich red almost as brilliant as that of the male, and altogether different from the ordinary Pierine white or yellow. The females, however, of *A. celestina*, *A. clementina* (Fig. 10), and others, do not depart, like the males, from the ordinary facies of the group,* and are indeed, barely distinguishable from the females of *C. jacquinotii*, *C. alope*, and other species of *Catophaga*. The assemblage of species united by Mr. Distant as *Saletara* (including *S. panda*, *S. cycinna*, etc.) is undoubtedly an offshoot from the *celestina* group of *Appias*.

In the three last-mentioned genera, although the two series S and M are generally more or less traceable, and although in most cases a decided remnant of ancestral black persists along the costa of the forewing, there is as a rule no relic of the original ground-colour in the region of the disco-cellular nervules; that is to say, there is no discoidal spot or patch. In *Hiposcritia*, however, which is apparently an early and purely Indian offshoot of *Catophaga*, some species (as *H. pandione*) exhibit an incipient discoidal patch, still in connection with

* See Wallace, Trans. Ent. Soc. Lond., 3rd series, iv., p. 301.

the dark-coloured costa; in others (as *H. lalage*) this has become a distinct discoidal spot (Fig. 11). *Hiposcritia*, by its anal tufts, belongs decidedly to the *Catophaga* and *Appias* group; but the shape of its wings and the occasional persistence of dark ground-colour about the discocellular nervules indicate that its origin is to be placed somewhat far back towards *Huphina* and *Metaporia*.

Starting again from *Metaporia* and *Pontia*, we find in the small Siberian *P. leucodice* an unmistakable link between these genera and *Synchloe*. In *S. callidice*, which perhaps come nearest to *Pontia*, the female shows S and M in a well-defined condition, together with a large distinct discoidal patch; the nervures and nervules are also in many instances clothed with black scales. From *S. callidice* we can advance in one direction through *S. chloridice* to *S. glauconome*, *S. johnstonii*, and *S. hellica*; while *S. daplidice* and its immediate allies form another slightly divergent branch from *S. chloridice*. *S. callidice* again in all probability marks the point at or near which the assemblage of species grouped as *Ganoris* leave the main *Synchloe* stem; *G. napi* being no doubt the species which is closest to the original stock, as is shown by the large persistence of S and M, the tendency towards blackening of the nervures, the occasional indication of a discoidal spot, and the peculiar coloration of the underside of the hindwings. It is noticeable that *Ganoris* generally, including *G. napi*, retains the precostal yellow streak, which, though present in most species of *Synchloe*, happens to be absent in *S. callidice*.

Most species of the genus *Tatochila* strongly resemble *Pontia* in pattern (the resemblance between *Tatochila* and *P. leucodice* has been pointed out by Mr. Butler, Proc. Zool. Soc., 1872, p. 62), while *T. autodice* ♀ comes nearer to *M. agathon* than does any species of *Synchloe*. The whole neuration of *Tatochila* is very similar to that of *Pontia*; and even the peculiar arching of the 1st subcostal of the hindwing (well seen in *P. cratægi*) is a noticeable feature in *T. theodice* and other members of the same genus.* *Tatochila* may, therefore, be considered to be a derivative from the *Pontia* stem at a point somewhat further back than the existing species of *Synchloe*.

* See Mr. Butler's figures in Cist. Entom., vol. i., pl. iii., figs. 7 and 9.

A comparison of *Tatochila* (especially of *T. theodice*) with *Phulia nymphula* will show an almost exact identity of pattern, the correspondence extending even to the chevron-shaped spots of S in the hindwing, and to the peculiar triple striation of the nervules on the under surface. The neuration of *Phulia* is distinct, but not really far removed from that of *Tatochila*, some species of which show a near approach to its most remarkable feature; viz., the emission of the second radial from the subcostal, and the consequent obliteration of the upper disco-cellular. *Phulia* again is closely allied in structure with Mr. Moore's genus *Baltia*,* which, however, retains the short 3rd subcostal nervule lost by *Phulia* and several species of *Synchloe*. *Phulia* and *Baltia* are thus, in all probability, the terminal twigs of another branch which issued from the *Pontia* stem between the departure of *Tatochila* and *Synchloe*. *Neophasia menapia* appears to me to be an offshoot of the same stem at an earlier stage than *Tatochila*. It may possibly belong to the *Eucheira* group, but it is not known to make a social web,† and Behr gives no real grounds for making it congeneric with "*N.*" *terlootii*. As above noted, its neuration is very distinct from that of *Eucheira*.

The African species of the genus *Mylothris*‡ appear to hold a somewhat isolated position. Their neuration shows points of likeness with the equally isolated Australian genus *Elodina* and the widely-spread and probably ancient *Nychitona*, ‖ which genera they also somewhat resemble in texture of wing. In pattern they are chiefly remarkable for the strong and distinct development of series M, and of the precostal orange-red

* Moore's type is "*Mesapia*" *shawii* of Bates, which is certainly generically distinct from *M. peloria*, and much nearer *Synchloe*. The butterfly described by Moore in Proc. Zool. Soc., 1882, p. 234, as *Synchloe butleri* is undoubtedly a *Baltia*.

† Stretch, however (Papilio, ii, pp. 106, 107), describes the larvæ of *N. menapia* as suspending themselves from great heights at the end of long silken threads. Even the pupæ were, in some cases, suspended. It is probable that the numerous threads covering the bark of the trees seen by Stretch (*ibid.*), were also made by these larvæ.

‡ I cannot but agree with Mr. Trimen (South African Butterflies, 1887, vol. iii., p. 29) that the American *P. pyrrha*, Fabr., and allies, are not generically akin to the African *M. agathina*, *M. chloris*, etc., with which Mr. Butler unites them on account of their correspondence in neuration (Proc. Zool. Soc., 1892, pp. 37, 38).

‖ Distant, Rhopalocera Malayana, 1882—1886, p. 287.

on the underside of the hindwing. We may, perhaps, regard all three genera as relics of an ancient fauna of the Eastern Hemisphere coeval with the earliest forms represented by the present *Delias* stock, and anterior to the various branches which have diverged from that genus or from *Metaporia*. The precostal orange suggests a kinship with *Delias* on the part of *Mylothris*, though no such link exists in the case of the other two genera, and, as pointed out by Mr. Trimen, who considers *Mylothris* and *Thyca* (*Delias*) to be allied genera, the former genus, like the latter, undoubtedly contains subjects of mimicry by *Pierinæ* of other groups. Thus, "The imitation of *M. agathina* by *P. thysa*, Hopff., is deceptively close in both sexes, and *M. poppæa*, Cram., is similarly copied by *P. rhodope*, Fabr., on the West Coast. *M. agathina* is also mimicked by the female *Eronia argia*, Fabr."*

We now have to deal with the genus *Belenois*, which presents some special difficulties. In the first place, we find an assemblage of species (*B. lasti*, *B. nagare*, *B. majungana*, and *B. isokari*) from East Africa and Madagascar, with respect to which Messrs. Grose Smith and Kirby, after noting that they are now placed with *Phrissura* in the Collection of the British Museum, go on to observe that they "differ entirely in neuration from the types of *Phrissura*, agreeing in this particular with *Belenois*, in which genus we prefer to include them."† The type of Mr. Butler's *Phrissura* is apparently *P. illana*, Feld.,‡ and in 1872 (Proc. Zool. Soc., 1872, p. 51) the only other species of *Phrissura* admitted by Mr. Butler was *P. polisma*, which is undoubtedly a very near relative of *P. illana*. Both of these species offer differences in neuration from *B. lasti* and its allies.‖ Now,

* South African Butterflies, vol. iii., p. 39 (1887).

† Rhopalocera Exotica, Oct. 1892.

‡ Mr. Butler first gave it as *P. cynis* (Cist. Entom., iii., 1870, p. 49), but afterwards corrected it to *P. illana* (Trans. Ent. Soc. Lond., 1871, p. 171). Mr. Distant has since made *cynis* the type of his new genus *Udaiana*. (Rhopal. Malayan., 1882—1886, p. 286 and note).

‖ In *P. illana* (forewing) the discoidal cell is unusually short, the second subcostal starts from the end of the cell, and the second and third median nervules come off near together; in *B. lasti* the cell is of the ordinary length, the second subcostal is emitted before the end of the cell, and the second and third median nervules do not start particularly near together.

however, certain forms are included under *Phrissura* in the Collection of the British Museum (*P. phaola, P. sylvia, P. eudoxia,* etc.) which appear to me to agree in structural characters with *B. lasti,* and to differ from *P. illana.* If, therefore, Messrs. Grose Smith and Kirby are right (which I do not doubt) in separating *B. lasti,* etc., from *Phrissura* as represented by *P. illana,* I am strongly of opinion that *P. phaola, P. sylvia, P. eudoxia,** and *P. coniata* should go with them; and to this assemblage I would add every so-called *Belenois* that is furnished with anal tufts, together with "*Belenois*" or "*Glutophrissa*" *saba.* We should then have a natural group of African and Malagasy Pierines, between which there would exist no assignable difference in structure, while they would be all alike characterised by the possession of anal tufts like those of *Catophaga* and *Appias.* They may, perhaps, be considered as a section of *Belenois,* but to my mind they seem by their neuration, no less than by the obvious character of the anal tufts, to come much nearer to *Appias,* of which genus I am disposed to regard them as an African offshoot. The South American species *Glutophrissa poeyi, G. margarita, G. castalia,* etc., are very closely related to the present section.†

Although the structural affinity of the forms that have just been discussed with each other and with *Appias* seems undeniable, there is no doubt that in pattern they mostly show a marked divergence from that genus. This appears to be due to mimicry, the models for which are usually supplied by the genus *Mylothris.* Thus *B. lasti* is said by Messrs. Grose Smith and Kirby to be "nearest to *B. trimenia,* Butl."; the latter, however, is a true *Mylothris* with the characteristic neuration of that genus. Considerable resemblance also obtains (as mentioned above, p. 308) between *P. rhodope,* Fabr., and *M.*

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* *P. eudoxia,* Cram., is apparently identical with *P. sylvia* ♀, Fabr.

† Mr. Wallace (*loc. cit.,* p. 312) includes these American and African forms with *Appias, Catophaga,* and *Hiposcritia* in his genus *Tachyris.* For the purposes of the present paper it will perhaps be sufficient if I refer to the American and African species with Appias-like structure and anal tufts collectively as "*Phrissura B,*" while designating *polisma* and *illana* as "*Phrissura A.*"

poppea, Cram.* The peculiar facies of *G. saba* ♀ seems to be most likely due to mimicry of *Nyctemera apicalis*, a protected moth. Those members of the group that have not been affected by mimicry retain few traces of the original ground-colour, and present very much the appearance of an ordinary male *Appias* (*G. saba* ♂, *G. castalia*, etc.).

The other species usually included under *Belenois*, besides differing in points of structure† from those just discussed, show as a rule a greater persistence of dark ground-colour. Both S and M are usually present in fair development, either separate or fused, and the discoidal patch on the forewings is generally well marked. The markings in several species show a strong resemblance to those of *Synchloe hellica* and *S. johnstonii*; but notwithstanding this, I am disposed to think that *Belenois* proper really represents an offshoot of another part of the Old World Pierine stem, that, namely, represented by *Delias* and *Prioneris*. The distribution of dark and light ground-colour in such species as *B. mesentina* might easily be derived from those of *D. belladonna* and *D. eucharis*, and the underside of the hindwing in this and other forms of *Belenois* offers only slight modifications from that of *D. belladonna*. *B. peristhene* exhibits a curious resemblance on both surfaces to *D. nysa* which may perhaps be due to mimicry, although the ranges of the two insects only coincide for a small part of their extent; it is not improbably in any case an indication of real affinity. In neuration, those species of

* I adopt Mr. Trimen's unravelling of the strange confusion that surrounds the synonymy of *rhodope*, Fabr., and *poppea*, Cram. (South African Butterflies, vol. iii., p. 35, and note). The upshot no doubt is that a true *Mylothris* (*Papilio poppea* of Cramer according to Mr. Trimen) is closely copied by at least one Pierine of the "*B*" group of *Phrissura* (*Papilio rhodope* of Fabricius according to the same authority). I do not propose to embark upon the question further than to observe that the "Synonymic Catalogue" identifies the two, and that Mr. Trimen himself unfortunately speaks of *rhodope* in the text, when he must mean *poppea* (ibid. p. 35).

† Negatively by the absence of anal tufts, positively by the presence (in many) of anal hooks, also by the straight direction and greater relative length of the upper disco-cellular nervule in the forewing. In many species of this group, which we may designate *Belenois* proper, the first subcostal branch anastomoses with the costal.

Belenois in which the first subcostal is distinct are very near *Prioneris*, and the remainder seem to approximate to *Delias* by the partial loss of a subcostal branch, as well as by the contour and direction of the disco-cellular nervules. It is to be observed that some species of *Belenois* proper, like those of the "*Phrissura B*" group, are mimics of various species of *Mylothris*, as *B. thysa* of *M. agathina*. *Pinacopteryx* is probably a collateral or derived branch of *Belenois*; the female of *P. capricornus* retains S and M on both surfaces in a well-marked condition.

We now come to a large and important group of genera which appears to take origin from the older Pierine stock at a point nearest to the genus *Synchloe*. An early stage of divergence is reached by *Teracolus*;* many species of which show the primitive series S and M, together with the discoidal spot and the precostal yellow of the underside of the hindwing. The curious genus *Herpænia* is probably a survival of the links that once united *Teracolus* with *Synchloe*; in neuration it is intermediate between the two, and in pattern, together with aberrations peculiar to itself, it shows points of contact with both. The pattern of the upper surface in *Teracolus* is easily derivable from that of *Synchloe*, the nearest approach to *Synchloe* in this respect being made by the *Idmais* group; compare, for instance, *T. dynamene* with *S. hellica* ♀. But the passage from the underside of the hindwing in *Synchloe* to that of *Teracolus* is more difficult; *Herpænia*, however, enables us to bridge over the interval very fairly, for if *H. tritogenia* and *H. lacteipennis* be interposed between *S. glauconome* and *T. puellaris* ♀, the abruptness of the transition is removed. The pupa of *Teracolus* tends to be boat-shaped, with a sharply-pointed rostrum and large prominent wings†—which characteristics we shall find

* I follow Mr. Butler (Cist. Entom. vol. i., p. 36), with whom Mr. Trimen is in agreement (South African Butterflies, vol. iii., p. 82), in uniting *Teracolus*, *Idmais*, and *Callosune* under the single head of *Teracolus*.

† These features are not equally well developed in all species of *Teracolus*. They are very distinctly shown in pupæ of *T. erarne* (Coll. Hope); pupæ of *T. calais* (Coll. B. Mus.), on the other hand, are slender, less recurved, and nearer the *Ganoris* or *Synchloe* form. The pupa of *T. pleione* (Coll. B. Mus.) is stout, and not unlike that of *Gonepteryx rhamni*; compare Mr. Trimen's description, *op.*

in a greater or less state of development in all the genera of the particular group of Pierines now under discussion. Other features, which appear first in *Teracolus* and will be met with again later on in the history of the group, are the pinkish fringe of the wings in some species (as *T. wallengrenii*, and often in *T. protractus*) and the faint pinkish *Colias*-like spot or patch at the root of the cell in the hindwing underside of others (as *T. tripunctatus*, *T. cœlestis* ♀, *T. eupompe*, and *T. theogone*).

The genus *Ixias* follows easily upon *Teracolus*, the females of the two genera showing, as usual, a greater affinity in colouring than the males (compare, for instance, the males and females of *T. ione* and *I. marianne* *). Series S is often well preserved in *Ixias*, especially on the underside and in the female; the discoidal spots are also prominent, and begin on the lower surface to assume an ocellate character. In neuration, *Ixias* differs only slightly from *Teracolus*; while the pupa, as shown in drawings by Captain Boys of *I. marianne* and *I. evippe* (Coll. Hope), has the same characters as *Teracolus* in a more strongly-marked condition.

From the usual system of colours and markings in *Ixias*, there can be little doubt that that genus represents the transition from *Teracolus* to *Colias*. The underside of several species of the latter genus (for instance, *C. subaurata*) is strongly recalled by that of *I. marianne*, in which the *Colias*-like condition of the discoidal spots is one of the most noticeable features. The affinity suggested by the colour-pattern is borne out by the structure of the antennæ, which in *Ixias* show a distinct approximation to the gradually thickened form so characteristic of *Colias* and its immediate allies. The pupa in *Colias*, as in *Teracolus*, seems to vary somewhat in form; but in all known cases it shows a tendency, sometimes strongly pronounced, towards the acuminate and boat-shaped outline characteristic of this group of genera.

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cit., vol. iii., p. 82. I refrain from using the terms "wing-covers" or "wing-cases," the inapplicability of which has been shown by Prof. Poulton (Trans. Linn. Soc., 1890, series ii., vol. v., part 5, p. 188).

* Mr. Butler points out the intermediate character of the two African species, *Ixias eulimene* and *I. venatus*. Proc. Zool. Soc., 1871, p. 254.

The genus *Xanthidia* is transitional between *Colias* and *Terias*, in neuration coming nearer the latter. The pattern on the upper side is scarcely modified from that of *Colias*; on the under surface, however, S has lost much of the distinctness it possesses in so many species of the latter genus, and its relics take part in a general mottling which is very probably protective in object.

In *Terias* the resolution of series S and M, which is still visible in most of the females and many of the males of *Colias*, has usually disappeared from the upper surface; the underside of the hindwings, however, generally shows S in a somewhat modified condition. The pink edging to the wings, so characteristic of *Colias*, and occasionally visible in *Xanthidia nicippe*, is indicated in several species of *Terias*, as *T. messalina*, *T. delia*, and *T. rhodia*. The pupa of *Terias* is more sharply acuminate and recurved than that of *Colias* (see pupa of *T. mandarina* and *T. excavata* in Coll. B. Mus.).

Sphænogona presents in pattern no marked differences from *Terias*, with which genus it is so closely allied. *S. gratiosa*, like *T. agave*, *X. nicippe*, and some other species of these genera, shows a relic of the pinkish *Colias*-patch at the root of the cell on the underside of the hindwing. In neuration, *Sphænogona*, while generally resembling *Terias*, is peculiar in emitting the first and second subcostal branches of the hindwing from a short footstalk beyond the end of the cell. In this respect it is intermediate between *Terias* and *Leucidea*, which latter genus presents no markings to guide us, but has no doubt taken its origin directly or indirectly from *Terias*.* Another probable descendant of *Terias* is the genus *Nathalis*, which agrees very fairly with *Terias* in neuration, except that it wants one nervule in the forewing, probably a branch of the subcostal. There is a striking resemblance of pattern between *N. iola* and *T. elathea* ♂. In the absence of paronychia *Nathalis* reverts to the condition of *Colias*.

Pyrisitia seems to represent an early offshoot of the stem leading from *Colias* to *Terias*. In most points it

* Staudinger and Schatz (*op. cit.*, Theil. ii., p. 66, etc.) consider *Leucidea* to be more closely related to *Pontia* (*Nychitona*) than to *Eurema* (*Terias*). The balance of evidence seems to me to be against this view.

agrees with the latter genus, but in the position of the subcostal nervules of the hindwing it retains the condition of the former.

A fresh departure from *Colias* is headed by the genus *Meganostoma*, which offers a close resemblance to *Colias* in both structure and pattern.* The series S and M, fairly distinct in the female of *M. philippa*, are also indicated on the upper surface in the males of some of the species. In the males of some other species they are fused above, but in all they are distinguishable beneath. In the outline of the wings *Meganostoma* shows a close approach to *Gonepteryx*, from which genus indeed the females of some of the species are hardly to be distinguished.

From *Gonepteryx* the line passes on to *Amynthia* and *Rhodocera*. All these genera retain many *Colias*-like points, particularly the pinkish patch at the apex of the cell on the hindwing undersurface. The males of the two latter, like those of *Meganostoma* and many species of *Colias*, also possess the well-known patches of raised scales above the subcostal nervure of the hindwing; and in the same two genera is seen for the first time the contrast between areas of flat and raised scales over the whole upper surface of the wings which is so conspicuous a feature in *Catopsilia*, *Phœbis*, and *Callidryas*.

Dercas appears to be an Indian offshoot of *Gonepteryx*. A good transition from the latter to the former is afforded by *D. wallichii*, as pointed out by Mr. Wallace, Trans. Ent. Soc. Lond., 3rd series, iv., p. 398. *Kricogonia* is probably an analogous derived form in the Neotropical Region.

The Eastern genus *Catopsilia* forms with the Western *Callidryas*, *Aphrissa*, *Metura*, and *Phœbis*, a group which clearly belongs to the present section. Their structure and coloration relate them closely to *Gonepteryx*, though in some respects they show signs of a more ancient

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* Mr. Butler (Cist. Entom., iii., p. 46) describes the neuration in the forewing of *Meganostoma* as being like that of *Gonepteryx*, "excepting that the second subcostal is emitted just before the end of the cell." In some individuals, at any rate, the second subcostal is emitted *at* the end of the cell, and in *M. cesonia* it may even be thrown off *after* the end of the cell, as often in *Colias*. This indeed is the condition represented in Cist. Entom., vol. i., pl. ii., fig. 4.

ancestry. The retention of the pink patch on the underside of the hindwing, and (in several species) of the pink fringe, brings them near to *Colias*; to which they also approximate by the form of the antennæ, by the very general occurrence of special patches of raised scales on the hindwing of the males, by the frequent presence, especially in the females, of the series S and M and the discoidal spots in a more developed condition than that characteristic of *Gonepteryx*, and by the common tendency of the latter spots on the lower surface towards ocellation. The oldest forms of the whole group appear to be those contained in the genus *Catopsilia*. *C. florella*, for example, is very closely related to *Gonepteryx*, and still more nearly to *Amynthia*, with which it corresponds in colour and in texture of wings (compare especially the undersides of *C. florella* ♂ and *A. clorinde*). The peculiar thickening of the nervures, especially the subcostal and median, on the under surface of the hindwing, which in *Gonepteryx* and *Amynthia* give almost the effect of a folding of the surface, is plainly visible in *C. florella*. In neuration, *C. florella* agrees minutely with *A. clorinde*. Another indication of the superior antiquity of the Eastern *Catopsilia* as compared with the Western *Callidryas* is found in the shape of the pupa. This in *Catopsilia* (as remarked by Mr. Trimen, *op. cit.*, vol. iii., p. 184) is only moderately acuminate and slightly recurved, thus showing no very great departure from the *Colias* and *Gonepteryx* form; in *Callidryas*, however, so far as is known, it is always very sharply acuminate and strongly recurved, showing an exaggeration of the "boat-shaped" condition almost as marked, in a different way, as that of *Euchloe*.* The *Colias*-like pink edging appears also to be found more frequently in *Catopsilia* than in *Callidryas* (though it occurs in *Callidryas sennæ*); and while the *Colias*-like spot at the root of the cell on the underside of the hindwing occurs in both the Eastern and the Western divisions of the group, it has in the latter lost the ancestral pink tinge

* I agree with Mr. Butler that the pupa figured in Lep. Exot., pl. xlv., fig. 4*a*, as *P. agarithe* is very probably that of *C. philea*. It closely resembles a pupa of *C. eubule* in the Hope Collection, which last exactly corresponds with Burmeister's figure in the "Atlas de la Description Physique de la Rép. Argent.," 1880, pl. v, fig. 2.

which it usually retains in the former. It is not very easy to form an opinion as to the relative antiquity of the four Western genera; if we are to judge from the pupæ, so far as they are known, it would seem that *Aphrissa* has undergone less modification than either *Phœbis* or *Callidryas*. Another possible indication of the greater antiquity of *Aphrissa* is afforded by the shape and size of the palpi, which in this genus, especially in the females, show less departure than is the case in either *Phœbis*, *Metura*, or *Callidryas*, from the *Colias* and *Gonepteryx* type. *Phœbis* with its offshoot *Metura*, from which it differs only in the contour of the wings, is probably the most highly specialised genus of all; this being shown by the possession of a tuft of long hairs on the hindwing of the male, which is not found in *Aphrissa* and *Callidryas*, and by the absence in most species of nearly all indication of dark ground-colour from the upper surface. It is remarkable that the Western genera just treated of are less closely akin to the South American *Amynthia* than is the Eastern genus *Catopsilia*, and especially the African *C. florella*.

The genus *Eronia* seems to represent a branch of the present section which leaves the main stem somewhere between the points marked by *Teracolus* and *Ixias*. With the exception of the presence of a fifth subcostal in the forewing (which, however, is sometimes wanting), the neuration of *Eronia* agrees fairly with that of *Teracolus*. The antennæ in *Eronia* differ in different species, but are all intermediate between the *Teracolus* and the *Colias* type; and the pupa of *E. cleodora*, with its very convex and prominent keel, is like that of one of the stout forms of *Teracolus*, e.g., *T. evarne*. The assemblage of species distinguished by Mr. Butler as *Nepheronia* is probably older than *Eronia* proper, as is shown by the tendency of its antennæ to terminate in a definite club, like the more ancient genus *Teracolus*. *N. thalassina* also retains a primitive Pierine feature in the yellow precostal streak of the hindwing underside, which again is found in some species of *Teracolus*. *Eronia* proper, on the other hand, is slightly nearer to *Teracolus* in neuration. The curious *Eronia* (?) *lucasii* from Madagascar, which has only four subcostal nervules in the forewing, and whose antennæ are slender, with a definite club, is probably one of the oldest and most

generalised members of the *Eronia* and *Nepheronia* group now extant.*

The last-named insect presents points of resemblance with *Hebomoia*, which again seems to be an offshoot of the same stem, that, namely, leading from *Teracolus* towards *Ixias* and *Colias*. The pupa of *Hebomoia glaucippe*, as figured by Horsfield (E. I. C. Catalogue, see Distant, Rhopal. Malayana, 1882—6, p. 283) and Moore (Lep. Ceylon, 1880—1, pl. 49, fig. 1*b*), is stout, moderately acuminate, and much recurved, in which particulars it agrees well with the pupa of *Ixias*.

Most of the insects of the genera *Eronia*, *Nepheronia*, and *Hebomoia*, retain in greater or less measure some portions of the primitive marginal and submarginal series. These, as usual, are most often to be met with in the females, and in several species of *Nepheronia* are utilised in the formation of mimetic patterns modelled on those of various Danaids and sometimes of other Pierines. A noticeable feature in some members of this group, pertaining chiefly to the males, is the brightening of the pale ground colour of the apex of the forewing into a brilliant yellow or orange patch. This character is first seen in *Teracolus*, where the orange of the apex may further deepen into crimson or violet; it passes on to *Hebomoia*, to *Ixias* and to *Rhodocera*; in *Colias*, however, it gives place to a general yellow or orange suffusion of the pale ground colour, still strongest in the males.† It is found in *Eronia* (?) *lucasii* and *E. leda*, but not in other members of that genus; it is also absent in *Nepheronia*.

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* *E.* (?) *lucasii* was originally described (as *Callidryas lucasi*) by Grandidier (Rév. et Magas. de Zool., Aug. 1867, p. 273). He, however, took the female for the male, and his supposed female *C. lucasi* is really the female of *Catopsilia thauruma*. Mabille in the Hist. Phys. Nat. et Pol. de Madagascar, vol. xviii., 1887, p. 281, gives a correct description of both sexes under the name of *Eronia lucasii*, but makes no mention of Grandidier's mistakes. This species will not come into the genus *Eronia* as at present defined. By Brauer and others it has been called a *Ptychopteryx*; the latter genus, however, was characterised by Wallengren from a species of *Teracolus* (*T. subfasciatus*, Swains., Vid. Trimen, South African Butterflies, vol. iii., 1889, p. 92), and has no real claim to stand.

† In many species of the latter genus, indeed, the females may, as is well known, revert almost entirely to the ancestral white.

This last feature in coloration is again met with in *Eroessa* and *Euchloe*, the neuration of which genera corresponds pretty closely with that of *Eronia*, not only in the presence of five subcostal branches in the forewing, but also in other particulars. The general likeness between *Eronia leda* and *Euchloe belia*, Linn., is very striking, and strongly suggestive of a near affinity between them. The well-known form of the pupa in *Euchloe* is an exaggeration of that seen in *Eronia cleodora*.* In some other points, however, *Euchloe* is nearer to *Colias*, as in the strong development of the discoidal spot in the primaries, and in the possession by some species of pink legs and a pink edging to the wings. This last feature is characteristic of the *charlonia* group of *Euchloe*, and is best seen in *E. lucilla*. The underside of the hindwing in the same group has very much the character of the corresponding region in *Colias palæno*, including the pale undeveloped discoidal spot. The antennæ, however, of *Euchloe* are very distinct in form from those of *Colias*, and indeed are not much nearer those of *Eronia*. On the whole it seems most likely that *Euchloe* is a somewhat aberrant branch which takes its rise from the Pierine stem at a point near the divergence from the same stem of *Hebomoia* on the one hand, and *E.* (?) *lucasii* with the rest of the *Eronia* and *Nepheronia* group on the other. The isolated form *Eroessa chilensis*, which in neuration approaches the older *Eronias* (as *E.* (?) *lucasii*) and *Hebomoia*, is perhaps a survival of a once more widely-spread and numerous assemblage, among which were to be found the immediate ancestors of the present-day *Euchloes*. *Zegris* seems to be a somewhat highly modified offshoot of the *Euchloe* branch.

We must now retrace our steps as far as to the group which I have called "Pierines of the second grade," those, namely, that are typified by *Delias* in the Eastern and *Catasticta* in the Western hemisphere. The latter genus with its near ally *Leodonta* forms a starting-point for a New-World division of the Pierine stem, which, if not equal in magnitude to the great division headed in the

* The pupa in *Euchloe* is not always recurved. See Edwards's figures of *Anthocharis* (*Euchloe*) *genutia* and *A. ausonides* in "Butterflies of North America." See also Schatz, Exotische Schmett., Theil ii., 1892, p. 71.

Old World by *Delias*, *Prioneris*, and *Metaporia*, is nevertheless of high importance and very great interest.

The first departure from the condition of *Catasticta* seems to be that taken by the butterflies of the genus *Pieris* as restricted by Butler, closely associated with which must come the American species of *Mylothris*. The underside of *Pieris locusta* exhibits a pattern which is but little removed from that of *Catasticta*, the yellow streaks and red basal patches being still apparent on the underside of the hindwing; while the upper surface of both wings is shared between the original dark and intrusive light ground colour in much the same manner as in *C. ctemene*, *C. corcyra*, and other species of *Catasticta*. In *Pieris* as a whole, the dark ground-colour has to a great extent disappeared from the upper surface; several species however (as *P. pylotis* and *P. buniæ*) retain a discoidal spot in the forewing, which in some, as *P. thaloe* ♀, is connected with a dark streak along the costa, and in others, as *P. demophile* ♀, is included in a larger remnant of ground-colour which passes as a dark fascia obliquely across the wing from the costa to the outer border. The underside of the hindwing in this genus tends to lose the *Catasticta*-like character preserved in *P. locusta*, in consequence of a general paling which takes effect first in the basal half and spreads outwards (as in *P. demophile*), until in such species as *P. buniæ* it reduces the wing to very much the same condition as that seen in *Ganoris brassicæ* or *G. rapi*. The ground-colour in *P. buniæ* and *P. pylotis* is indeed even paler than in these species of *Ganoris*, being without the powdering of black scales which the latter possess; the hindwing however of both *P. buniæ* and *P. pylotis* retains a discoidal spot, and, as has been already noted (pp. 287, 289, note), the predominance of the paler colouring is never so great as not to leave unmistakable relics of the yellow streaks and red basal patches.

The genus *Leptophobia* appears to be a kind of continuation of *Pieris*. The arrangement of light and dark ground-colour preserves a parallel course in the two genera, and the inclusion of the discoidal spot of the forewings in a dark fascia which passes from the costa for a greater or less distance obliquely towards the outer margin is a common feature in *Leptophobia* as well as in *Pieris*. In the present genus the underside of the hind-

wings is almost uniformly pale, but distinct indications of the primitive red patches are nevertheless still to be met with (see p. 287).

There would also seem to be little doubt that the American species allied to *M. pyrrha*, which are included by Mr. Butler* under *Mylothris*, with the neuration of which they agree, are closely related to *Pieris*. The pattern of every one has been more or less altered by mimicry, but in those males whose upper surface is unaffected by this kind of modification, the arrangement of the dark and light ground-colour is seen to present the ordinary features of *Pieris* or *Leptophobia* (compare, for instance, the upper side of *M. pyrrha* ♂ with that of *P. thaloe*). In *M. lorena* is found an oblique dark bar crossing the forewing just as in *P. demophile* and *L. stamnata*, this mark being utilised, both in *M. lorena* and the female of *M. pyrrha*, for the formation of the mimetic pattern. It has already been shown† how the primitive yellow streaks and red basal patches have been turned to account in the same direction on the underside of the hindwing, which, from the additional necessity for protection experienced by the insect when at rest with its wings closed, becomes the most important field for the mimetic process. It may be here remarked that the antennæ of these American forms, while agreeing in character with those of *Leptophobia*, *Pieris*, *Catasticta*, *Leodonta*, and the genera allied to these last, differ conspicuously from those of *M. agathina*, *M. poppea*, and the other African species of *Mylothris*.

Hesperocharis diverges somewhat widely from the genera last discussed, both in neuration and in the character of its antennæ; it retains, however, in many cases indications of the primitive marginal and submarginal dark series in a more recognizable form than any (see, for instance, the chevrons on the underside of *H. erota*, which represent series S). The yellow streaks

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* Proc. Zool. Soc., 1872, pp. 36-38. It appears to me that the neuration of the American forms of *Mylothris* is simply that of *Pieris*, *minus* the third subcostal nervule in the forewing, which branch is already almost obsolete in the latter genus.

† See above, p. 286. The transitional series which is there made to begin with *M. lypera* and *M. lorena* might easily be carried back to *P. thaloe*, which shows the true Pierine pattern all ready, as it were, to take on the mimetic condition of the other species.

and red basal patches, present in all species of *Hesperocharis*, are in some (as *H. nereis*) marked with special distinctness. The curious manner in which these have been made use of in *H. hirlanda* for the production of a mimetic pattern, has already been fully discussed (p. 286).

I cannot but think that *U. monuste* shows by its pattern that it stands on a level with *Pieris* as a derivative from the *Catasticta* group. Its neuration hardly differs from that of *Pieris*, and it would probably be more appropriately placed (together with its immediate allies, *U. joppe*, *U. suasa*, etc.) in or near that genus than with *U. cynis* in Mr. Distant's genus *Udaiana*, as at present in the National Collection.

The position of the genus *Dismorphia* is not easy to determine. The pattern of those species that appear to have undergone least modification may, however, be derived without much difficulty from *Pieris* or *Leptophobia*;* and the persistence in some cases of the red basal spots has already been remarked (see p. 285). The structure of the antennæ points to the same line of ancestry. On the other hand, the very remarkable neuration is quite unlike that of *Pieris*; a certain approach to it, however, is made by *Hesperocharis*, which is almost without doubt a close ally of that genus. *Moschoneura*† is very nearly akin to *Dismorphia*, from which it differs only slightly in neuration; while the Palæarctic genus *Leptosia* has characters which link it with both.‡ We may probably regard the three last-named genera as terminal twigs of a branch now lost, which left the main stem at or near the genus *Pieris*, and of which *Hesperocharis* is a still earlier offshoot. In *Dismorphia* and a few species of *Moschoneura* much of the original colouring has been retained and modified for purposes of mimicry. In *Leptosia* and the remainder§ of *Moschoneura* this colouring has given way to the usual Pierine invasion of white.

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* A somewhat different and, as it seems to me, less probable view is advanced by F. Müller, Jenaische Zeitschr., x., pp. 1–12.

† The figure in Cistula Entomologica, vol. i., pl. iv., fig. 9, omits the second discoidal of the forewing.

‡ The forewing is nearer to *Dismorphia* and the hindwing to *Moschoneura*.

§ *Pseudopieris* of Godman and Salvin.

2. *The evidence of distribution.*

It now remains to briefly indicate the bearing of the geographical distribution of the various forms that have been mentioned upon the question of their kinship and relative antiquity.

As we have already seen, the oldest form of Pierine now extant is probably *Eucheira socialis*. This insect appears to be as limited in its geographical range as it is isolated in its zoological position, for it is found only in the mountain-ranges of Mexico, which may be considered as a southern extension of the "Rocky Mountain" division of the Nearctic Region.* Its nearest allies appear to be Behr's two species of *Neophasia* (see p. 303), which inhabit the same region with itself, and the *Pontias* and *Metaporias* of the high lands of Central Asia, most of which forms are known to retain the ancient larval habit of spinning. These facts seem to point to the conclusion that *Eucheira* is the relic of an archaic group of Pierines which once occupied the great mountain regions of both the Palæarctic and Nearctic continents, and whose immediate descendants, still represented in the East by *Metaporia* and *Pontia*, have in the West become extinct (unless Behr's *Neophasia* be a survival) after giving origin to the group of genera headed by *Catasticta*.

From one or other of these two primary stems, the Eastern or the Western, nearly the whole of the existing genera of Pierines may be derived. There are, however, a few exceptions, which, perhaps, constitute relics of an ancient Pierine fauna coeval with the groups above mentioned, but not, like them, the progenitors of a numerous and varied offspring. The chief of these are the genera *Elodina* and *Nychitona*, the former of which is entirely confined to the Australian Region, while the latter has a very wide distribution throughout the Ethiopian, Oriental, and Australian. The African

* I here follow Mr. Sclater's division of the earth's surface into six Zoological Regions, which arrangement, adopted by Mr. Wallace in his "Geographical Distribution of Animals," 1876, has stood the test of time and experience better, in my opinion, than any alternative distribution that has been proposed. I also adopt, for convenience, the smaller divisions, or "sub-regions," as determined by Mr. Wallace in the above-named work.

species of *Mylothris* belong possibly to the same category.

The genera derived from the *Catasticta* group remain, for the most part, within the confines of the Neotropical Region. This is the case with *Pieris, Leptophobia, Hesperocharis,* the American species of *Mylothris,** *Dismorphia, Moschoneura,* and those species allied to *monuste* at present included in the genus *Udaiana.*† It is remarkable that the Nearctic Region does not furnish a single species that can be supposed to be derived from the present stem.‡ Inasmuch, however, as the Palæarctic genus *Leptosia* seems to belong rather to this than to any Eastern branch, the conjecture may be hazarded that connecting forms now extinct once occupied the Nearctic Region, from which the Palæarctic continent received the forerunners of its present *Leptosias,* probably by way of Behring Strait.

Turning now to the Eastern *Metaporia,* which inhabits the borderland between the Palæarctic and Oriental Regions, we find it emitting one clearly-defined branch in the Palæarctic direction. This is the branch to which belong the various species of *Pontia,* as *P. nabellica, P. soracta, P. hippia, P. belucha, P. leucodice,* and *P. cratægi.* In the Chilian or Andesian division of the Neotropical Region we find the genus *Tatochila,* which appears not to belong to the regular Neotropical Pierine stock, but to be closely related to the Palæarctic *Pontias.* It is conceivable that the latter stem may have spread from Asia into the western portion of the Nearctic continent, and thence down the mountain-chains to the south. *Neophasia menapia,* at present inhabiting the Californian and Rocky Mountain subregions, seems to me to be more nearly allied to both *Pontia* and *Tatochila* than (as Behr thinks) to *Eucheira socialis,* and may very possibly be a relic of the original invasion. Another indication of the same invasion is afforded by the genus *Phulia,* now found with the nearly-allied *Tatochila* only in the Andesian or Chilian

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* See p. 320, note.

† See p. 321.

‡ The instance of *U. monuste*, which straggles into the southern districts of the Nearctic Region, hardly forms an exception to the above statement.

sub-region, to which it no doubt made its way along the great mountain-chains in a similar manner. Its close ally, *Baltia*, remains in the high lands of Central Asia, where it bears much the same relation to *Synchloe* as *Phulia* to *Tatochila*. Another early offshoot from the Eastern *Pontia* stem is *Mesapia peloria*,* which has no representative in the Western Hemisphere.

The above descendants of the mountain *Metaporias* belong, as has been seen, in the first place, to the Palæarctic and western portion of the Nearctic Region, only reaching the Neotropical by extension along the chain of the Andes. Other derivatives of *Metaporia*, however, took their course directly southwards. The first of these is the *Delias* and *Prioneris* group, the more ancient members of which are, speaking generally, to be found in the northern portion of the Indian peninsula, while the Australian and other southern forms represent, as a rule, a somewhat later stage of development. Another is the important branch headed by *Huphina*, which genus, like *Delias*, has spread downwards throughout the Oriental Region, and by way of the Indo-Malayan and Austro-Malayan islands to the Australian continent. The Australian species of *Huphina* are clearly derived from the Oriental, and those forms (such as *H. phryne* ♀) which are nearest to *M. agathon* in colouring are also its closest neighbours geographically. Of the two genera (*Hiposcritia* and *Catophaga*) which appear to be immediately derived from *Huphina*, the former is confined to the Oriental Region; while the latter, like *Huphina* itself, has spread along the Austro-Malayan Islands to the Australian mainland. This is also the case with *Appias*,† the origin of which genus from the *Catophaga* stock is no doubt to be assigned to the Oriental Region. But, unlike the other genera, *Appias* seems to have extended its borders westwards, and to have given rise to the "*Phrissura B*"‡ group in the Ethiopian Region, and even to *Glutophrissa* in the Neotropical. If this be the real origin of these two latter genera, we have to enquire how they reached the African and South American continents respectively.

* See p. 304.

† It would seem, however, that no true *Appias* actually reaches the Australian continent.

‡ See p. 309, note.

With regard to the first, there is little difficulty in supposing the passage to have been effected by land either now or formerly existing, the Ethiopian Region having been in this, as in so many other instances, first entered from the north. But it is not easy with our present knowledge to imagine an overland passage for these butterflies from the Oriental or Ethiopian Region to the Neotropical. The northward route, which we saw to be the one probably adopted by the ancestors of the Chilian *Phulias* and *Tatochilas* in spreading from Central Asia, is excluded in the present instance by the entire absence of any trace of such a passage from both the Palæarctic and Nearctic Regions; and although a transit by way of a formerly existing "Antarctica" is conceivable, it would seem more likely that the crossing from east to west was effected in the region of the tropics. After all, however, the difficulty of supposing an Atlantic sea-passage is not overwhelmingly great. The unusual facilities possessed by insects for crossing large extents of sea have been remarked by many writers,* and among insects the butterflies of the Pierine group are especially given to migration for great distances in countless hordes.† It is worth noting that in the case of each of the other three chief Pierine genera whose present distribution seems to have involved one or more long sea-passages, *i.e.*, *Terias*, *Colias*, and *Callidryas*, special observations exist of their migratory propensities. In 1874 a large swarm of *Terias lisa* reached the Bermudas from the American continent;‡ the swarm of butterflies described in a well-known passage‖ by Mr. Darwin consisted chiefly of a species of *Colias*; while descriptions of the migratory flight of *Catopsilia* and *Callidryas* are numerous, among the most striking pieces of testimony being that

* See especially Wallace's "Geographical Distribution," 1876, vol. i., p. 32; and the same author's "Darwinism," 1889, p. 359, etc.

† Trimen, Trans. Ent. Soc. Lond., 1870, p. 382; "South-African Butterflies," 1887, vol. iii., p. 32. Moore, "Lepidoptera of Ceylon," 1880, 81, p. 116. Distant, "Rhopalocera Malayana," 1882—86, p. 285, etc. Mr. Trimen suggests that there is "an evident connection or relation between these wonderful migrations of certain species of *Pierinæ* and the well-known habit of nearly all the members of the Sub-family of flying straight onward in one direction."

‡ "Psyche," Dec. 1875, p. 121.

‖ "Voyage of the Beagle," ed. 1860, p. 158.

of Mr. Spruce, who saw *Callidryas* "launching boldly out over the Pacific Ocean."*

The earliest species of *Synchloe* were undoubtedly differentiated from *Pontia* or *Baltia* in the Palæarctic Region, from which the genus spread (probably eastwards) into the Nearctic. *Synchloe* proper can hardly be said to enter the Indian Region,† but in its progress westwards it has sent an offshoot downwards into the Ethiopian, consisting of *S. johnstonii* and *S. hellica*. *S. glauconome* of Arabia and Egypt remains to mark the course of the invasion. *Ganoris*, a further Palæarctic development of *Synchloe*, has accompanied that genus into the Nearctic Region and has also spread into the Oriental. A curious extension of the range of the Palæarctic *G. rapæ* into the Nearctic Region has been in progress during the last thirty-three years, the first transatlantic specimens having been seen at Quebec in the year 1860.‡ This introduction was undoubtedly effected by human agency, and differs from the natural passage of species between the two Regions in having taken place by the Atlantic instead of the Pacific route.

Though *Synchloe* itself is far more characteristic of temperate than of tropical districts, it has given rise to a large and important Pierine branch which has spread far and wide through tropical and temperate parts alike. The birthplace of *Herpænia* and *Teracolus*, the two earliest members of this extensive section, is apparently the eastern portion of the Mediterranean division of the Palæarctic Region; from which locality the former has spread through Arabia and Abyssinia into the African continent, while the latter has not only followed *Herpænia* into Africa, but has also largely occupied the two western Oriental sub-regions. Those forms of the genus *Ixias* that show least divergence from *Teracolus* are found in the Nile provinces of Eastern Africa, but the bulk of this genus has moved eastwards, its distribution being characteristically Indian. A few species, however, are found in some of the Indo-Malayan islands, and in Austro-Malaya as far east as Timor.

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* Journal Linn. Soc., Zool., ix., pp. 355—357.

† See Wallace, Trans. Ent. Soc. Lond., 3rd series, iv., pp. 242, 3.

‡ Scudder, "Butterflies of the Eastern United States," 1889, vol. ii., pp. 1175-1190; Edwards, "Butterflies of North America," vol. i., 1868-72, *sub. voc. P. virginiensis.*

To the same borderland of Western Asia and Eastern Africa may be assigned the place of origin of *Nepheronia*, which has sent a western branch into Africa, and an eastern into the Indian peninsula and Malayan islands, one species reaching the Australian continent. The African branch has given rise to *Eronia* proper. Attention has already been drawn to the curious fact that the form which links the *Eronia* group most closely with *Teracolus*, viz., *E.* (?) *lucasii*, survives in Madagascar. *Hebomoia*, another offshoot of this part of the Pierine stock, is now almost entirely Malayan; its place of origin was, however, in all probability further west. The birthplace of *Euchloe* is problematical, but the present distribution of the *charlonia* group, which seems to contain the oldest members of the genus, would appear to make it probable that the Mediterranean sub-region witnessed the rise of this, as of so many other more or less direct descendants of *Synchloe*, from which central area it successively overspread the Palæarctic and Nearctic continents. The isolated geographical position of *Eroessa chilensis* is very remarkable, its affinities being apparently with Eastern rather than Western forms. It is probably, as before suggested, a solitary survival of a once more widely-spread group, among which were to be found the immediate ancestors of the present-day *Euchloes*.

No other genus in the whole sub-family has so extensive a range as *Colias*, species of which are found in every one of the six great Zoological Regions. Here again, I have little doubt that the site of original divergence is Asiatic, and is most nearly represented in the present condition of the earth's surface by the borderland between the Palæarctic and Oriental Regions on the north-west frontier of India. From this centre one or two species have ranged into South Africa and the Indian peninsula; but the greater number have turned northwards, and after populating the Palæarctic and Nearctic continents with numerous species, have penetrated to the circumpolar lands within the Arctic Circle, have passed down the great mountain chains of Central and South America to Chili and Patagonia, and have even established outposts in Venezuela and the Sandwich Islands.*

The powers of dispersal possessed by the genus *Terias*

* The occurrence of *Colias* in the last-named locality is, however, not entirely free from doubt.

are almost as remarkable as those of *Colias*; perhaps even more so when we take into account their weak flight, and the fact that their migrations must have been intertropical. Mr. Wallace, however, has drawn attention to their habit of frequenting "gardens and plantations and skirts of forests rather than their deeper recesses," and also of "assembling on the margins of streams and on the sea beach," and has remarked that "these habits lead to their being frequently carried off by winds," and that "it is thus perhaps that some of the species have so wide a range and offer such perplexing variations."* Whatever may have been their means of dispersal, there can, I think, be no doubt that they took their rise from the *Colias* stock in the Western Hemisphere, the line of descent passing through *Xanthidia* to *Terias* and *Sphœnogona*; *Pyrisitia*, *Nathalis*, and *Leucidea* being given off by the way. All these genera are mainly Neotropical with Nearctic extensions. *Terias* itself, however, as is well known, so far from remaining within these limits, has overspread the warmer portions of the Ethiopian, Oriental, and Australian Regions, and is even found in the Manchurian sub-region of the Palæarctic.

It seems on the whole most probable that the origin of *Gonepteryx* is also to be referred to the Western Hemisphere, where *Meganostoma* marks the transition from *Colias*. *Gonepteryx* itself seems to have passed to the north by way of California and so across into the Palæarctic Region, while *Rhodocera* and *Amynthia* represent a Neotropical development of the same stock, the Central American genus *Kricogonia* perhaps remaining near the original seat of divergence. *Gonepteryx* having reached the Palæarctic Region has extended to its westernmost extremity. Its only offshoot appears to be *Dercas*, which probably arose in the debateable Manchurian area, where the Palæarctic and Oriental faunas are much mixed, and thence spread southwards through the Indo-Chinese sub-region to Sumatra and Borneo.

Catopsilia and *Callidryas*, like *Terias*, must, it would seem, have undergone intertropical migration. Their oldest forms appear to be *Catopsilia florella*, *C. hyblæa*,

* Trans. Ent. Soc. Lond., 3rd series, iv., p. 320. See also above, p. 325.

C. thauruma, etc., which are probably derived from the Neotropical genus *Amynthia*, coming nearest to *A. clorinde*. Inasmuch as all these are African insects, and the New World *Callidryas*, *Phœbis*, and *Metura* are less closely allied to *Amynthia*, it seems necessary to suppose that the earliest forms of this group in the Neotropical Region have become extinct, the present *Callidryas* group surviving as their modified descendants; while an early dispersal of these ancestral forms took place across the Atlantic to Africa, of which invasion *C. florella*, etc., remain as comparatively unmodified relics. The Oriental and Australian *Catopsilias* are the ultimate developments of this invasion.

The distribution of *Belenois* is remarkable, the bulk of the species belonging to the Ethiopian and Australian Regions. The Oriental Region is poorly supplied, except for the abundant *B. mesentina*, which is found in all parts of the Indian peninsula, and even enters the Mediterranean district of the Palæarctic Region as far as Asia Minor. Notwithstanding the present poverty of the Oriental Region in species of *Belenois*, it seems probable that this area is really the birthplace of the genus, which, as we have seen, appears to be derived from that primitive part of the Pierine stem now represented by *Delias* and *Prioneris*. *B. mesentina* and *B. taprobana*, of India and Ceylon, may probably be regarded as survivors of the original race of *Belenois*, whose descendants have spread south-eastwards to Australia, and south-westwards to Madagascar and the African continent. *Pinacopteryx* is in all probability a local modification of *Belenois* within the Ethiopian Region, while *Daptónura*, whose history is otherwise hard to account for, may perhaps have originated from a branch of the African *Belenois* which at some remote period found its way westwards across the Atlantic.

In concluding this paper I wish to express my great indebtedness to several friends who have given me valuable help during its progress. It was by the kindness of the late Professor Westwood that I was enabled to begin the study of the Pierine group in the Hope Collection at Oxford, and the facilities for work afforded me by him have been continued and increased by his successors in the charge of the department, first by

Mr. W. Hatchett Jackson, and now, in a special manner, by Professor Poulton, F.R.S., the present occupant of the Hope Chair, at whose request I have undertaken the arrangement of this part of the Hope Collection. I am also under great obligations to Colonel Swinhoe, who has very kindly helped me in various ways, and especially in the determination of the Eastern species, of which he has so intimate a knowledge. Lastly, my thanks are due to the members of the staff of the Natural History Department of the British Museum, particularly to Messrs. A. G. Butler, W. F. Kirby, and F. A. Heron, who have given me every assistance in examining the fine series of *Pierinæ* preserved in the National Collection.

IV.—Index of Species Mentioned.

The Order is that of the National Collection in the British Museum.

Pierinæ.

* Probably not a *Mylothris* ; see Trimen, "South-African Butterflies," vol. iii., 1889, p. 35, note.

Danainæ.

Heliconinæ.

EXPLANATION OF PLATES III., IV., & V.

PLATE III.

FIG. 1. *Eucheira socialis.*
2. *Catasticta bithys.*
3. *C. ctemene.*
4. *Delias belladonna.*
5. *D. eucharis* ♀.
6. *D. nysa* ♂.
7. *Metaporia agathon.*
8. *Huphina phryne* ♀.

PLATE IV.

FIG. 9. *Catophaga paulina* ♀.
10. *Appias clementina* ♀.
11. *Hiposcritia lalage* ♂.
12. *Mylothris agathina.*
13. *Belenois mesentina* ♂.
14. *B. peristhene.*
15. *Synchloe daplidice* ♀.
16. *Ganoris napi* ♀.

PLATE V.

FIG. 17. *Teracolus hewitsonii.*
18. *Ixias marianne* ♀.
19. *Hebomoia glaucippe* ♀.
20. *Colias hyale* ♀.
21. *Catopsilia crocale*, var. *flava* ♀.
22. *Callidryas philea* ♀.*
23. *Eronia leda* ♀.
24. *Euchloe charlonia.*

These figures are only designed to illustrate the actual points mentioned in the text. They are not intended to show specific characters. The same letters and numbers stand for the corresponding markings throughout all the figures. See explanations in the text, pp. 254, 264, 269, 273, 274.

NOTE.—In Fig. 15, S 8 is placed one space too high up.

* This figure was drawn from a specimen in the Hope Collection, which had been erroneously labelled *C. thalestris.* The error has unfortunately found its way into the plate.